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POPULATION DYNAMICS AND ECOLOGY OF SUBARCTIC SHREWS

by

© DAVID M. DOYLE

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

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Supervisor

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Date....21 Nov 79.....

Abstract

Populations of four species of shrews (Soricidae) were studied from May, 1976 to December, 1977 on 4-ha pitfall removal grids and pitfall trap lines in the taiga south of Great Slave Lake, N.W.T. Sorex cinereus reached peak numbers in the summer of 1977 from a low in 1976; S. arcticus numbers increased slightly in 1977 while Microsorex hoyi and S. obscurus numbers remained stable. The numbers of sympatric voles, Microtus pennsylvanicus and Clethrionomys gapperi, were out of phase with S. cinereus as they synchronously peaked in 1976 and crashed in 1977. The 1975-76 winter had high and uniform subnivean temperatures while the S. cinereus prepeak winter (1976-77) had low and fluctuating temperatures. Thus, the summer abundance of shrews did not seem to be governed by the subnivean microclimate.

During the summer, shrew populations, except for S. obscurus, consisted of two age groups, young of the year and overwintered animals, which were readily separable by means of their tooth height index. Overwintered males greatly outnumbered overwintered females, while young of the year animals tended to have an even sex ratio. The greater activity of overwintered males associated with breeding was probably responsible for their abundance in pitfall catches.

The breeding season extended from late April to

September, but reproductive activity declined sharply after mid-July. The mean litter size was approximately eight for M. hoyi, S. cinereus, and S. arcticus while a pregnant female with six embroyos was the only indication of litter size for S. obscurus. Young of the year females of all species were observed to mature sexually only in 1977 when environmental conditions were considered to be favourable, but only S. cinereus came close to realizing its full reproductive potential as revealed by its peak numbers. No young of the year males were observed to mature sexually.

Shrew populations were confined to lowland habitats for most of the year. Increases in population numbers of S. arcticus and particularly S. cinereus, sympatric in shrub birch fens, resulted in dispersal of young of the year animals into black spruce fens and upland areas by late summer. M. hoyi and S. obscurus populations which tended to be sympatric in black spruce fens remained at relatively stable levels with minimal dispersal. Since most shrew species appear to be territorial, their population density seems to regulate the number of animals in suitable habitats and allows only a certain number to overwinter successfully.

The distribution of shrew catches on the removal grids revealed that M. hoyi and S. cinereus preferred moist microhabitats whether tree cover was open or closed and avoided dry sites. S. arcticus had similar preferences but seemed to be able to tolerate dry areas. All three species

preferred areas with dense ground cover.

Overwintered animals were longer, heavier, and had lower craniums than young of the year animals for M. hoyi, S. cinereus, and S. arcticus. There were also some sexual differences, which in the case of S. cinereus suggested sexual dimorphism, females being larger than males. The seasonal variations in body length, weight, and cranial height revealed the occurrence of Dehnel's phenomenon in these Nearctic shrew species, confirming that this phenomenon is characteristic of Holarctic shrews. It is hypothesized that taiga shrew populations are controlled by energy limitations, particularly those imposed by winter conditions which limit their distribution and their spring population levels.

Acknowledgements

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My thanks go to Dr. W.A. Fuller, graduate students, and assistants for providing shrew specimens from upland trapping activities. Steve Beare provided assistance in the initial preparation of the study grids; Lorne Duncan aided in the setting of early summer trap lines in 1977; and Simon Pickering ran the grids in the fall of 1977. The histological technicians at the University of Alberta instructed me on the techniques used in the examination of reproductive tracts. Rainfall data were supplied by the Mackenzie Forest Service.

Special thanks are given to Dr. W.A. Fuller for support during the study and editing of thesis drafts. Dr. R. Hudson aided in the multivariate statistical analysis used to analyze vegetational cover preferences of shrews. Numerous friends and my committee advisors, Dr. R. Hudson and Dr. V. Lewin, made comments and suggestions.

Finally, I am grateful to my wife, Bernice Doyle, for moral support, assistance in every aspect of the field work, and typing of thesis drafts.

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Introduction

The numbers of many small rodent populations fluctuate in a cyclic manner (Krebs and Myers 1974), while annual fluctuations occur in numbers of small insectivores. Population cycling in microtines has been investigated by many in search of mechanisms that regulate population numbers, but it would seem that the question of population regulation would be more relevant to shrews. What limits the numbers of these animals which are so highly specialized for their insectivorous habit (Pernetta 1977) and have a high metabolic rate as a result of their small body size? The answer would seem to be related to the high energy requirements of these animals. Shrews have become efficient predators exploiting a high protein food source, soil invertebrates, with which they satisfy their energy requirements.

Population studies of subarctic shrews in North America are scarce. Buckner (1966) and Iverson and Turner (1976) studied shrews in eastern Manitoba while Polinsbee (1971) studied introduced Sorex cinereus in Newfoundland. In contrast, Eurasian researchers have contributed much to our understanding of shrew population dynamics. It is now up to North American researchers to determine whether the population dynamics of Nearctic species of shrews are similar to those of Palearctic species. It has long been

known that seasonal morphological changes occur in Palearctic shrews (Dehnel's phenomenon) but almost nothing is known concerning this phenomenon in Nearctic species. If these changes in body weight, length, and cranial height are adaptations to long, snowy winter conditions (Mezhzherin 1964), they would be expected to occur in North American species.

The objectives of the present study are to describe the population dynamics and ecology of four species of subarctic shrews with emphasis on:

1. the effect of microclimate on the relative abundance of sympatric species of shrews and small rodents;
2. the winter biology of Nearctic shrews in relation to Dehnel's phenomenon; and
3. habitat and microhabitat preferences in the different shrew species.

Morphological changes in shrews are discussed as an adaption to taiga winter conditions. This has led to the hypothesis that shrew populations are controlled by the energy limitations imposed by their environment, especially during the winter period which annually limits their distribution and their spring population levels.

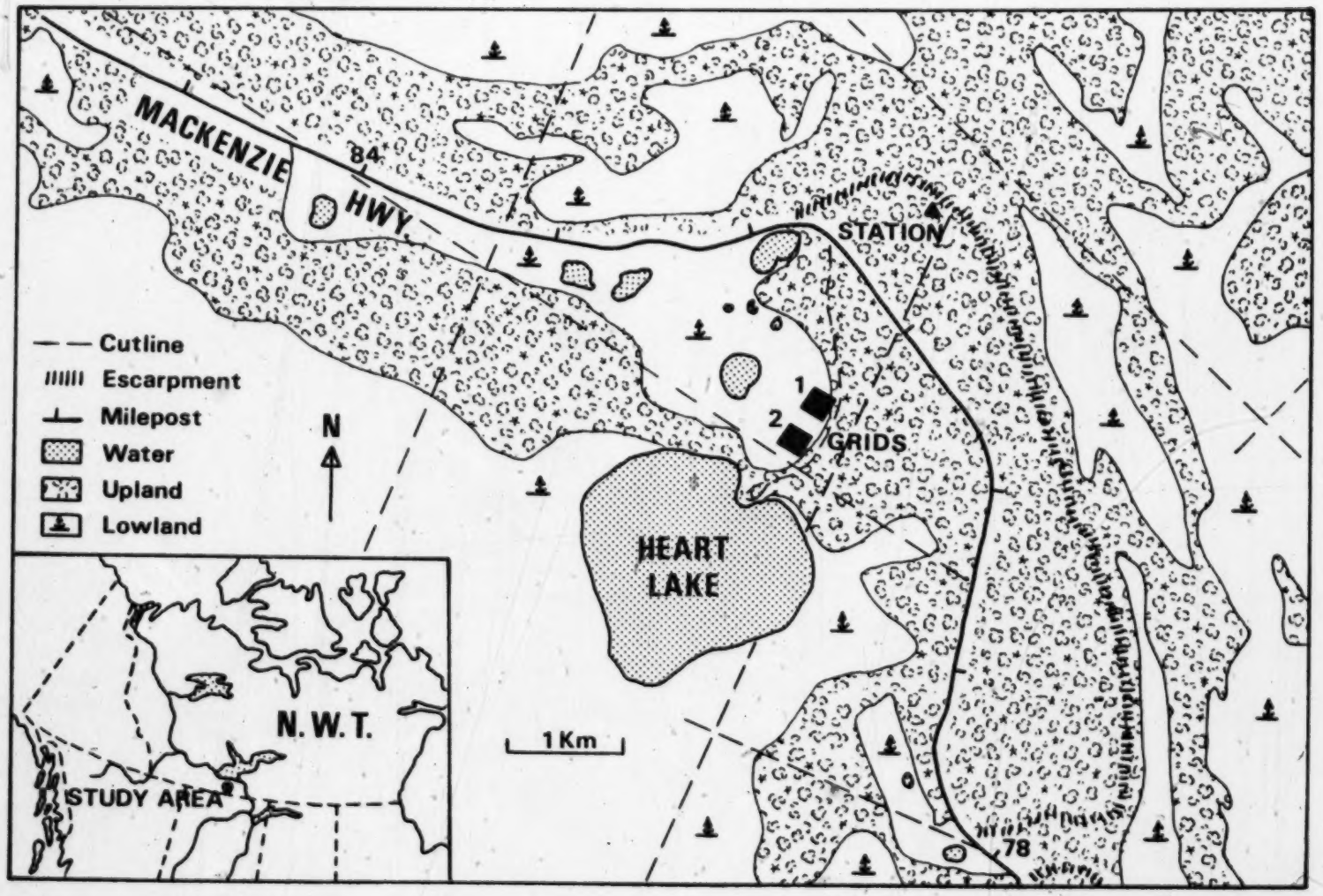
Study Area

The field work for this study was conducted at the University of Alberta's Heart Lake Biological Station (60° 52' N, 117° 22' W) southwest of Great Slave Lake, in the District of Mackenzie, Northwest Territories, Canada from 1976 to 1977. The primary study area was approximately 3 km southwest of the Research Station near Heart Lake (Fig. 1). From Heart Lake (249 m ASL) the land gradually rises to about 270 m at the Research Station and then drops off to 230 m below a steep limestone escarpment. The escarpment edge, which the Mackenzie Highway follows, forms the boundary between the Mackenzie Lowlands to the north and the Alberta Plateau to the south.

The open black spruce (Picea mariana) and scattered tamarack (Larix laricina) wooded fen covering the removal grids is typical of the poorly drained lowlands of the Hay River section of the boreal forest (Rowe 1972) occupying the Alberta Plateau. Two other major components of the lowlands are raised ombrotrophic plateau bogs and reticulate string fen (Cody and Talbot 1978). Coniferous and mixed forests of white spruce (Picea glauca), jack pine (Pinus banksiana) and trembling aspen (Populus tremuloides) cover upland areas.

The major soils series of the area, as described by Day (1968), are the Matou, Desmarais, Enterprise and Escarpment. Desmarais and Matou soils, which occur in lowland areas, are

Figure 1. Map of the study area showing the location of the removal grids, Heart Lake Research Station, and major physical features.


MACKENZIE HWY
84
STATION
Cutline
Escarpment
Milepost
Water
Upland
Lowland
N
1
2
GRIDS
HEART LAKE
1 Km
N.W.T.
STUDY AREA
78

peaty deposits over gravelly loam and mineral soils, respectively. The study was conducted on areas of Matou soil which develop in poorly drained basins and have permafrost within 45 cm of the surface. The Heart Lake area is within the discontinuous permafrost zone (Brown 1970) and it is in these boggy areas with their thick insulating mat of Sphagnum that permafrost is found.

The Enterprise and Escarpment soil series occur on upland beach deposits of sand and gravel. The organic layer is extremely thin with the Escarpment soils overlying a rock base, that is exposed in many areas.

The Heart Lake area is within the Cold-Temperature Boreal Zone of Troll and Poffen (1964). The climate can generally be described as harsh, cold and continental. The winters are long, cold and dry, while summers are short and warm.

Removal Grids

Removal grids were located in a wooded fen just west of an esker which formed the border between upland and lowland areas (Fig. 1). The ground slopes gently to the west creating a moisture gradient. This area is characterized by hummocky relief with water accumulating in the depressions, especially in the spring.

Black spruce is the dominant tree while tamarack is scattered. Labrador tea (Ledum groenlandicum) is the characteristic shrub species while shrub birch (Betula glandulosa), bog rosemary (Andromeda polifolia), juniper (Juniperus horizontalis) and cinquefoil (Potentilla fruticosa) are common. Ground cover consists of fruticose lichens (Cladonia) on the drier hummocks with mosses (Hylocomium splendens and Tomenthypnum nitens) in the moist depressions. In very wet areas (west end of grids) Sphagnum fuscum forms large mats around the bases of trees. Growing up among the mosses are horsetails (Equisetum), bearberry (Arctostaphylos rubra), cranberry (Vaccinium vitis-idaea), creeping willow (Salix myrtillifolia), crowberry (Empetrum nigrum), and a variety of graminoids. A great many small mammal burrows are visible, especially at the bases of hummocks.

Pitfall Trap Lines

During the first summer (1976), and the spring of 1977, trap lines were located in wooded black spruce fens while for the rest of the study, shrub birch fens were selected. These areas are almost treeless with very dense shrub cover and hummocky relief. The few trees present are tamarack. Shrub birch and sweet gale (*Myrica gale*) are the dominant shrub species with some patches of willow. Graminoids form the next stratum beneath the shrubs. A relatively thick leaf litter layer replaces most of the mosses and lichens. Depressions have standing water keeping the leaf litter moist. In 1976 the high water table put most of the ground surface of these areas under water.

Small Mammal Community

In addition to the four species of shrews studied, six species of rodents were also present in the small mammal community. The insectivore portion of the community consisted of three species of *Sorex* (*S. cinereus*, *S. arcticus*, and *S. obscurus*) and *Microsorex hoyi*. The rodents present were meadow voles (*Microtus pennsylvanicus*, red-backed voles (*Clethrionomys gapperi*), heather voles (*Phenacomys intermedius*), northern bog lemmings (*Synaptomys borealis*), meadow jumping mice (*Zapus hudsonius*), and deer mice (*Peromyscus maniculatus*). *S. obscurus*, *S. borealis*, and *Z. hudsonius* were uncommon in the Heart Lake area. *P. maniculatus* was rare in lowlands but abundant in uplands.

Methods

Relative Abundance

The changes in numbers of shrews and other small mammals were monitored by two methods. Removal grids measured the relative abundance of dispersing animals where as pitfall trap lines sampled populations in different lowland areas. The relative abundance of animals was expressed as numbers per 100 trap nights (TN). It must be remembered that both the abundance and activity of animals influence the numbers captured in pitfalls.

Removal grids

Two removal study grids were established 200 m apart within the primary study area. Each grid had 100 trap stations set 20 m apart in a 10 x 10 array. The grids were 4 ha in area including a boundary strip of 10 m around the outermost traps. Each station was marked by a numbered stake and orange survey flagging. This allowed capture points to be identified, and eliminated the possibility of missing traps. One continuous foot path was made from trap to trap, summer and winter, in order to minimize disturbance to the area.

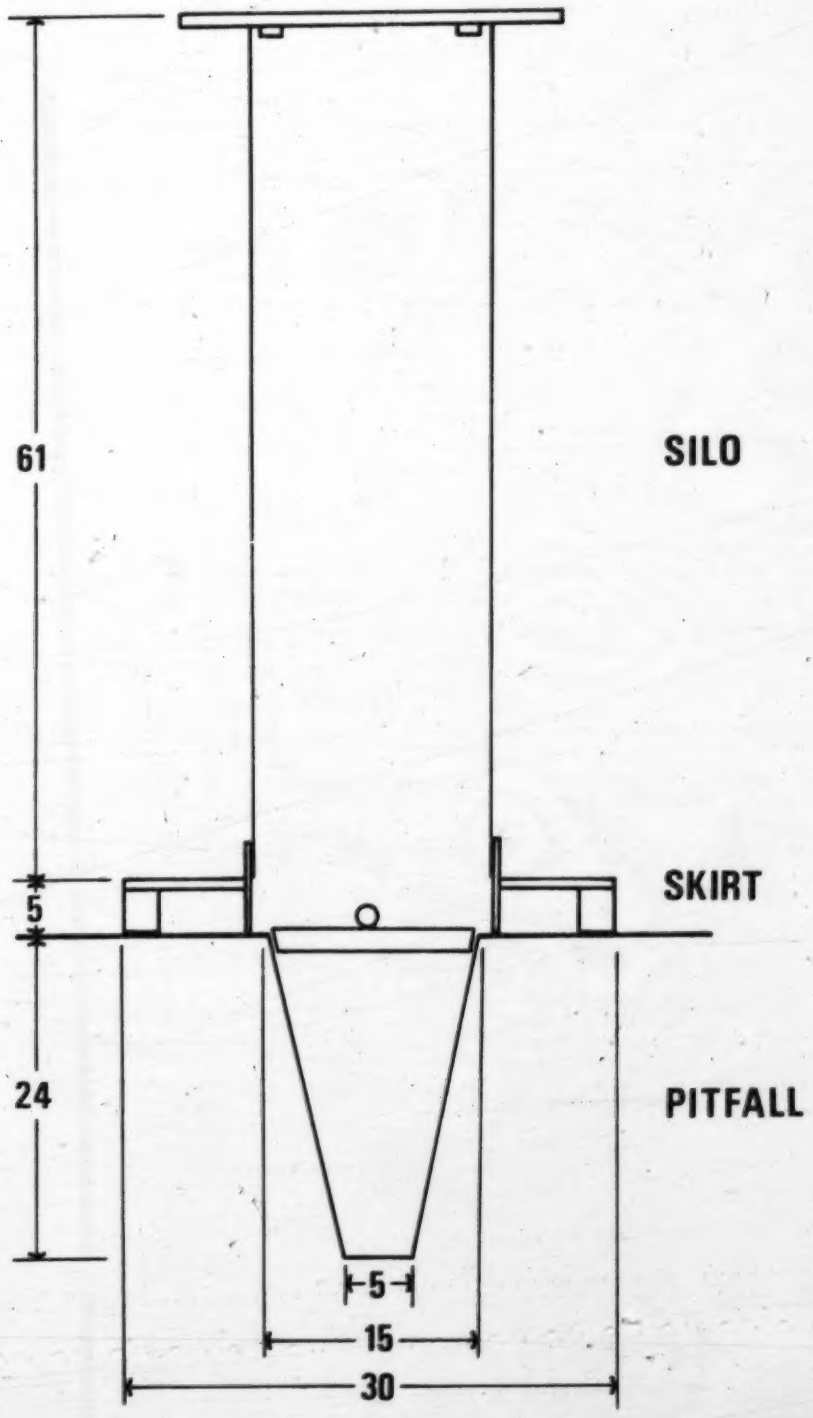
The traps were conical, sheet metal pitfalls with a flat bottom (Fig. 2). Such shape allowed them to be set into the ground easily or nested together for transporting. One pitfall was placed within 1 m of each surveyed location with its mouth flush with or just below the ground surface. In order not to disturb the immediate area around the pitfall, peat from the trap excavation was placed in a pile at the base of a nearby tree. It was possible in some areas to cut slits in the thick moss mat and push traps in. Each pitfall was rendered inoperative by means of a plywood lid between trapping periods.

Most pitfalls contained varying amounts of water because of the high water table. Holes in the bottom allowed water to enter and prevented traps from being forced up out of the ground.

Each grid was trapped for a 3-day period on alternate weeks from May, 1976 to December, 1977. With few exceptions the grids were operated from Monday to Thursday. The lids were removed from the pitfalls Monday mornings and the traps checked Tuesday, Wednesday, and Thursday mornings. Thursday the lids were replaced after traps were checked. All small mammals captured were placed in plastic bags numbered with the trap station and taken to camp for autopsy.

Winter trapping required certain equipment modifications but the general procedure outlined above

Figure 2. Diagram of the silo and skirt positioned over the pitfall for winter trapping. All measurements are in cm.


61
SILO
5
SKIRT
24
PITFALL
5
15
30

remained the same. Sheet metal silos fitted into plywood skirts were positioned directly over the pitfalls (Fig. 2) before the first snowfall. This allowed access to the subnivean space and pitfall via the silo without seriously disturbing the snow cover. A hooked length of wire was used to remove and replace circular lids from the pitfalls, before and after trapping periods. The lids over the silos were only removed to check the traps, which was done with the aid of a flashlight. Captured animals were retrieved by a 4-clawed mechanical arm. Since only 100 silos were available, every second trap was used on each grid and the others were closed. Silos were removed and all traps were used as soon as spring snow conditions permitted.

Trap lines

Various lowland habitats were sampled during the summer months by means of pitfall trap lines. The trap lines were located within the study area south of the Mackenzie Highway from milepost (MP) 78 to MP 84 and at least 500 m from the grids. Lines of 20 or 25 traps, spaced at 10 m intervals, were run from three to four days within a single habitat. Traps were checked every morning and animals captured were placed in plastic bags and later autopsied.

Trap lines were not used until August, 1976, but they were used throughout the summer of 1977. In 1976, quart cans were used for pitfalls, which retained shrews but may not have held all the rodents. In 1977, sheet metal pitfalls,

like those used on the removal grids, were used on the trap lines. All trap lines were located in wooded black spruce fens until mid-June, 1977, after which they were placed in shrub birch fens.

Pitfall trapping was impossible in upland areas because bed rock was close to the surface. Shrews caught in snap trap lines run by W.A. Fuller and his students were used to calculate an index of relative abundance. However, it is well known that shrews are captured much more readily in pitfalls than in snap traps (MacLeod and Lethieq 1963; Brown 1967). Therefore, these indices must be examined with some caution.

Autopsies

Wet animals from pitfalls were allowed to dry and frozen ones to thaw before autopsies were performed. Shrews were weighed to the nearest 0.1 g on a triple-beam balance. Weights of visibly pregnant females were corrected by subtracting the weight of the reproductive tract. Animals partially eaten by other shrews or ants were not included in this part of the analysis. Standard measurements (total length, tail length, and hind foot) were recorded to the nearest millimeter. Body length was calculated by subtracting tail length from total length. Almost all measurements were done by myself except from September to

December, 1977, when S. Pickering, whom I instructed, measured the animals.

The sex and reproductive condition of each individual was recorded. In doubtful cases the reproductive tract was fixed in AFA and transferred to 70% ethanol after fixation. Histological preparations were serially sectioned from paraffin blocks at 7 µm, stained with Heidenhain's Haematoxylin and Eosin, and mounted in DPX (polystrene dissolved in xylene). Slides of histological preparations were examined under a compound microscope.

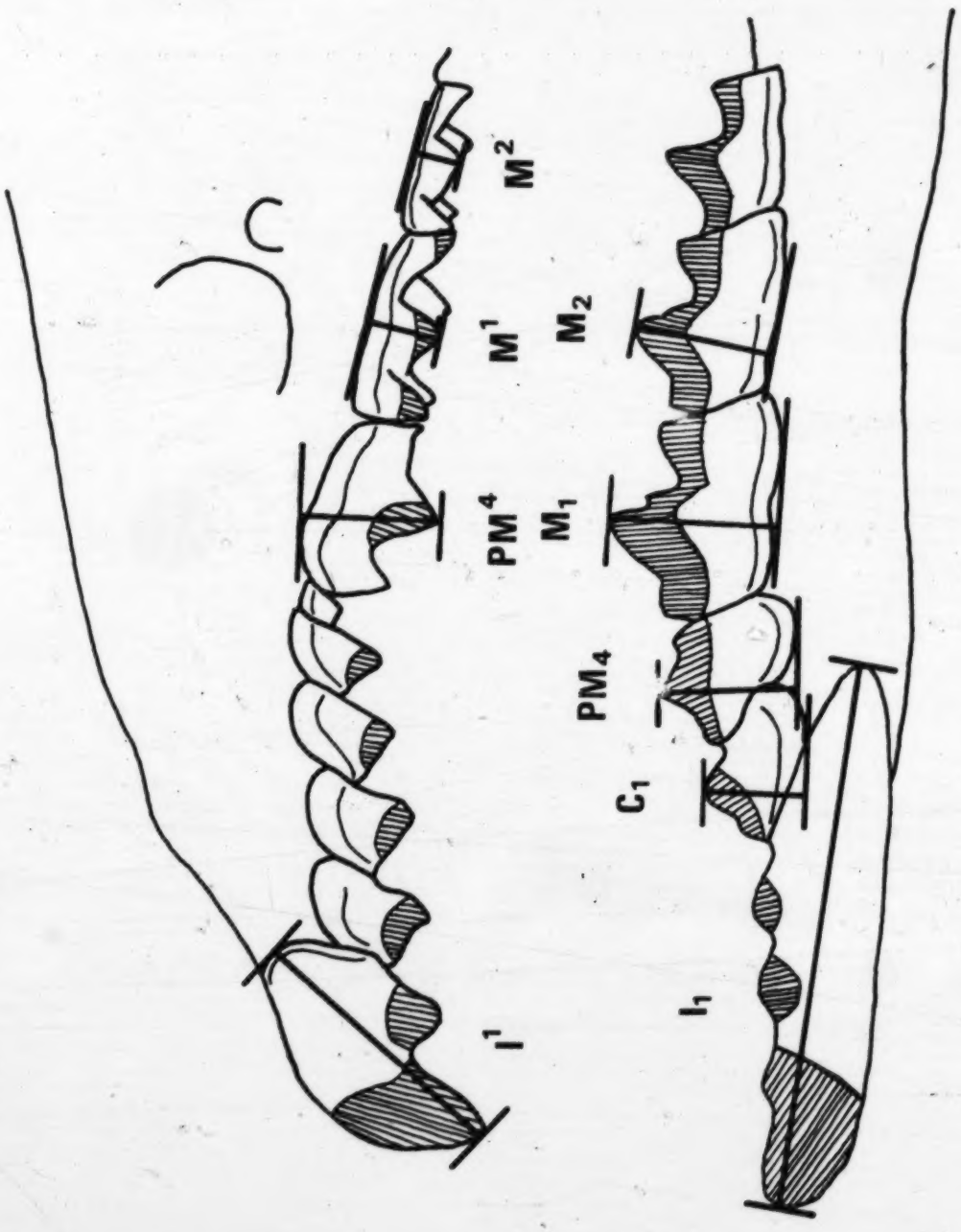
All skulls were saved for use in age determination and measurement of cranial height.

Aging And Cranial Height

Two basic methods have been used to determine the age of shrews:
(1) dividing skulls into toothwear classes (Jackson 1928; Hamilton 1940; Pearson 1945; Pruitt 1954; and others) and (2) measuring the teeth (Conaway 1952; Crowcroft 1956; Bishop and Delany 1963; Rood 1965; and Pernetta 1977).

I used a modification of the technique of Conaway (1952). For each skull, four tooth heights were measured from the left maxillary tooth row and five from the left mandibular tooth row (Fig. 3). All measurements were taken by means of an ocular micrometer in a dissecting microscope

Figure 3. Lateral view of the rostrum of a S. cinereus skull indicating the tooth measurements taken on all shrew skulls to determine a tooth height index.


C
I¹
PM⁴
M¹
M²
I₁
C₁
PM₄
M₁
M₂

at 10X power.

Variation in cranial height with age (Jackson 1928) and season (Dehnel 1949) was investigated using the method of Hawes (1975). The skull was placed on a glass slide so that it was resting on its front upper incisors and petrosal. The total height of the cranium and the glass slide was measured using vernier calipers. The thickness of the glass slide was measured separately and subtracted from the total to give the cranial height.

Temperature

Air and microenvironmental temperatures were measured daily between 9 and 11 A.M. from June, 1976 to September, 1977. Air temperatures were read from a maximum-minimum thermometer located in a protective screen 1.6 m above the ground. Microenvironmental temperatures were measured by means of thermistors on the surface, 3 cm below the surface, 30 cm below the surface, in shallow small mammal runways, and 30 cm down in a burrow. The labelled thermistor wires ran into the screen where they could by connected in sequence to a Yellow Springs Instrument telethermometer.

Maximum, minimum, and subnivean temperatures before June, 1976 were taken at the Heart Lake Station (W.A. Fuller, unpublished data).

Rainfall

Daily rainfall records were made available by the Mackenzie Forest Service from the Heart Lake Fire Tower approximately 3 km north of the study area. These records only covered the May to August period. For September the monthly total was taken from records of the meteorological station at the Hay River airport (Environ. Canada 1976, 1977). This station is in the Mackenzie Lowlands close to Great Slave Lake, approximately 73 km northeast of the study area. The difference in total monthly rainfall between the two areas for the May to August period was 3.1 ± 2.28 mm and 12.4 ± 1.93 mm for 1976 and 1977, respectively, with Heart Lake having the higher rainfall. Therefore, the September rainfall total from Hay River would be a conservative estimate for the Heart Lake area.

Snow

The snow studies were done near Grid 2 with a set of instruments from the National Research Council of Canada. The instruments and their use are described by Klein et al. (1950). Snow thickness and density were measured for every distinct snow layer every two weeks in an undisturbed area.

Snow measurements for the winter of 1975-76 (W.A. Fuller, unpublished data) were taken from a snow survey location north of the Mackenzie Highway near MP 83 (Fig. 1).

Microhabitat

The effect of microhabitat on the relative abundance of shrews was investigated by two methods.

First, within the wooded black spruce fen covering the removal grids, four qualitatively different microhabitats were recognized.

1. Open-dry: areas of hummocky relief with lichens being the major component of ground cover. Tree cover was sparse.
2. Closed-dry: lichen covered gravel ridges with tree cover of black spruce intermingled with jackpine.
3. Open-wet: open areas with mats of Sphagnum spreading out from the bases of trees present. The ground was water-logged with water filled depressions.
4. Closed-wet: areas of hummocky relief with mosses other than Sphagnum being dominant. The tree cover was composed entirely of black spruce.

The importance of these microhabitats on the distribution of shrews was determined by comparing the observed number of shrews captured in each with the expected (number if shrews were distributed randomly) by means of Chi-square (X^2).

Second, the effect of vegetation cover was examined by estimating the cover of the herb, moss, lichen, shrub, and tree strata. The sampling procedure used a 2 m circular quadrat centered at each trap station. Percent cover of each stratum was estimated and assigned a class value (Table 1).

Table 1. Cover classes.

Class	Percent cover
1	<1
2	1 - 5
3	6 - 25
4	26 - 50
5	51 - 75
6	76 - 100

The multivariate statistical method, Multiple Classification Analysis (MCA), was used with analysis of variance to analyze the interrelationships of shrew abundance and vegetational cover.

Statistics

The data were analyzed using the appropriate computer programs from the SPSS statistical package (Nie et al. 1975). Mean values are given with the standard error (±1SE).

MCA analysis is essentially a multiple regression technique using dummy variables (Andrews et al. 1973). The model specifies that a coefficient be assigned to each category (cover class) of each predictor and the number of shrew captures for each location be treated as a sum of the coefficients assigned to categories characterizing that location, plus the average for all cases (grand mean), plus an error term:

$$\hat{Y}_{ij\ldots n} = \bar{Y} + a_i + b_j + \ldots + e_{ij\ldots n}$$

where

$\hat{Y}_{ij\ldots n}$ = the number of shrew captures at location n which falls in category i of predictor A, category j of predictor B, etc.

$\bar{Y}$ = grand mean.

a_i = effect of membership in the i^{th} category of predictor A.

b_j = effect of membership in the j^{th} category of predictor B

$e_{ij...n}$ = error term

Results

Microclimate

Microclimatic data were divided into four periods of the year judged to be significant to shrews as well as other small mammals.

1) Fall transition
2) Deep snow
3) Spring thaw
4) Snow-free

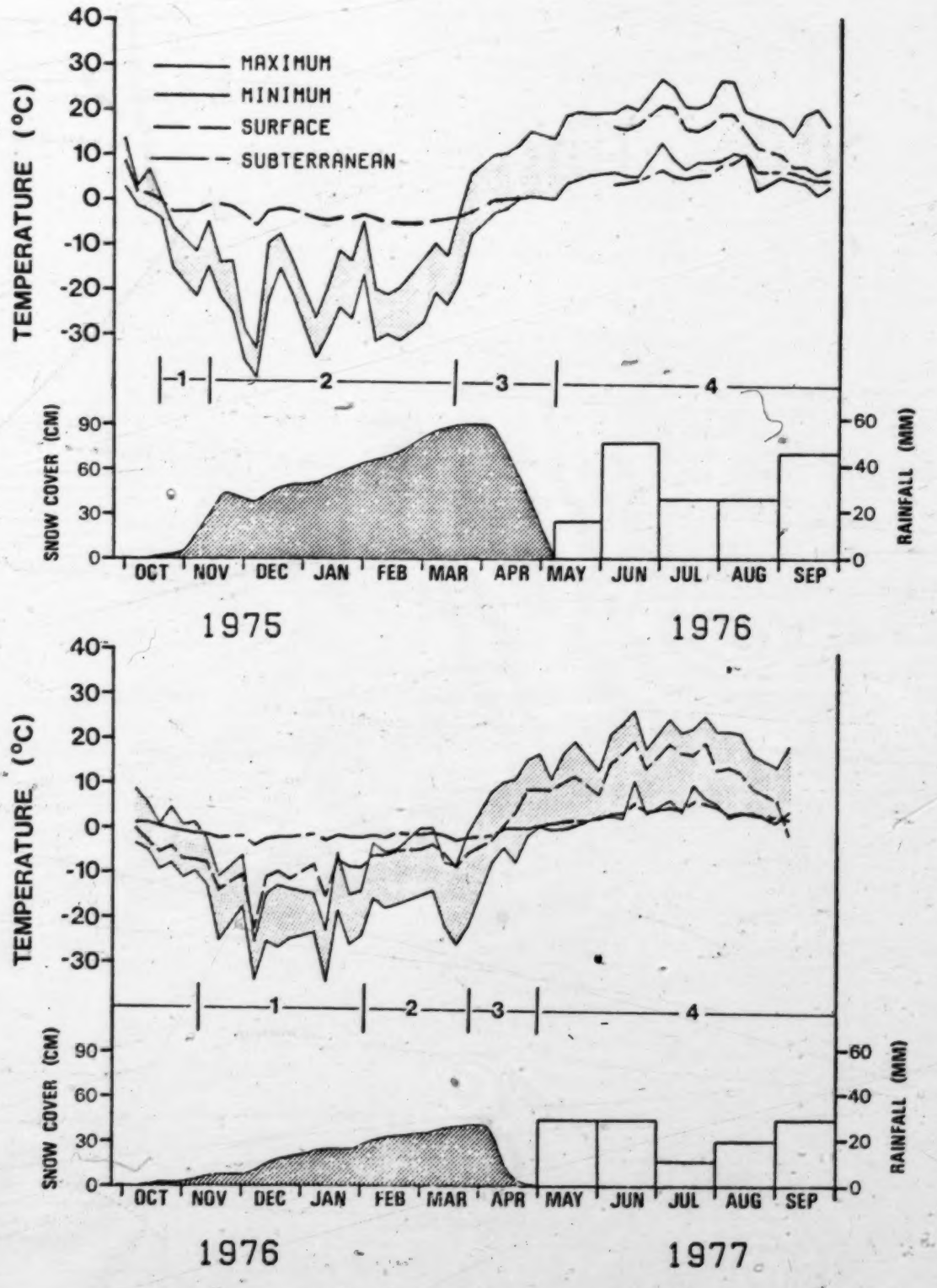
A summary of the microclimate for 1975-77 is given in Figure 4. The runway and burrow temperatures were the same as those at the ground surface and 30 cm below surface temperatures, respectively. Thus, only the surface and subterranean temperatures are presented.

Fall transition

Fall transition begins when the weekly mean maximum air temprature drops below 0° C and ends when the fluctuating moss surface temperature stabilizes with the accumulation of 30 cm of snow. This period is similar to the fall critical period of Pruitt (1957). Its length depends mainly on the rate of snow accumulation that insulates the moss surface.

The 1975 fall transition period was short and subnivean temperatures remained high. In contrast, 1976 had a lengthy

Figure 4. Summary of the 1975-77 microclimate. Weekly mean maximum air, minimum air, ground surface, and subterranean temperatures in relation to snow cover and rainfall. The periods presented are fall transition (1), deep snow (2), spring thaw (3), and snow-free (4).


TEMPERATURE (°C)
40
30
20
10
0
-10
-20
-30
MAXIMUM
MINIMUM
SURFACE
SUBTERRANEAN
1
2
3
4
SNOW COVER (CM)
90
60
30
0
RAINFALL (MM)
60
40
20
0
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
1975
1976
1976
1977

fall transition with low subnivean temperatures. Though conditions at ground level were harsh, subterranean temperatures were only a few degrees below freezing. Subterranean temperatures were not recorded in 1975 but they would probably have been similar. The 30 cm of moss insulation causes a temperature variation of only a few degrees around 0° C the entire year (Fig. 4).

Deep snow

The deep snow period is between the end of fall transition and beginning of spring thaw when snow cover is at least 30 cm deep and subnivean temperatures are stable. This period was four months long in 1975-76, and only two in 1977. Note that spring thaw began at about the same time each year so that the length of the period of deep snow was related, like that of the fall transition, primarily to the rate of snow accumulation. Over twice as much snow accumulated in 1975-76 as in 1976-77.

Snow density measurements for the winters of 1975-76 and 1976-77 are given in Tables 2 and 3, respectively. These measurements are limited due to the physical size of the instrument used; the sometimes thin surface layers could not be measured.

There were few thaws during the two winters so that snow cover was uniform and of low density, which provided excellent insulation once 30 cm had accumulated.

Table 2. Snow density data measured near MP 83 of the Mackenzie Highway, 1975-76 (Fuller, unpublished data).

Dates	Snow density (g/cm^2)			
	Surface layer	Layer 2	Layer 3	Layer 4
Oct 28	.16	-	-	-
Nov 19	.18	.18	-	-
Dec 3	.19	.18	-	-
17	.12	.19	-	-
Jan 3	.16	.20	.22	-
19	.10	.15	.20	-
Feb 3	.12	.16	.20	-
18	.14	.17	.20	-
Mar 3	.10	.15	.17	.20
16	.15	.20	.18	-
Apr 4	.17	.22	.27	-
17	.26	.41	-	-

Table 3. Snow density data measured near Grid 2, 1976-77.

Dates	Snow density (g/cm²)		
	Surface layer	Layer 2	Layer 3
Nov 30	.14	-	-
Dec 14	.11	.19	-
28	.15	.21	-
Jan 11	.12	.16	.17
25	-	.16	.18
Feb 8	.13	.21	-
22	-	.16	.24
Mar 8	.20	.26	-
22	-	.23	.26
Apr 5	.26	.18	.19

Spring thaw

Spring thaw is the period when the weekly mean maximum air tempratures rise above 0°C and the snow cover melts with flooding of the microhabitat. The spring critical period of Fuller (1967) corresponds to this time.

Extensive flooding occurred in 1976 with water covering low lying areas most of the summer. The 1977 runoff was brief; flooding was minimal.

The moss surface temperatures increased with air temperature and the disappearance of snow in both years. Subterranean temperatures only increased slightly in 1977 and probably would have exhibited the same trend in 1976.

Snow-free

The snow-free period was about the same length for both years. It begins with the disappearance of the snow cover and ends when the weekly mean maximum air temperature drops below 0° C, making a permanent snow cover possible. Without the insulative cover of snow, moss surface temperatures rose and fluctuated with air temperatures. Subterranean temperatures responded very slowly to the warm air temperatures, reaching a maximum of 10° C in August, 1976.

Except for May, every month in 1976 had greater rainfall than the corresponding month in 1977. June, 1976 and May, 1977 had over twice their normal monthly rainfall

(Environ. Canada 1976, 1977). As a result of the heavy rainfall and spring runoff in 1976 most lowland microhabitats experienced some degree of flooding during the snow-free period.

Age Groups

On the basis of the tooth height index it was possible to recognize two age groups for each shrew species (Fig. 5 and 6). Overwintered (OW) animals have a low tooth height number and have lived past December 31 of their year of birth. Young of the year (YY) have a high tooth height number and have not yet lived past December 31 of the first year.

There exists a great deal of variation within each age group. This is probably due in part to individual variation in tooth wear and to the difference in age of individuals caught during a particular period. Because the breeding season extends from April to September individuals caught at the same time may differ by several months in age.

Figure 5. Scattergrams of the tooth height indices of M. hoyi and S. cinereus. Three cohorts can be distinguished on the basis of tooth height: 1975 (closed squares), 1976 (half-open squares), and 1977 (open squares). OW animals have lower tooth height values than YY animals.

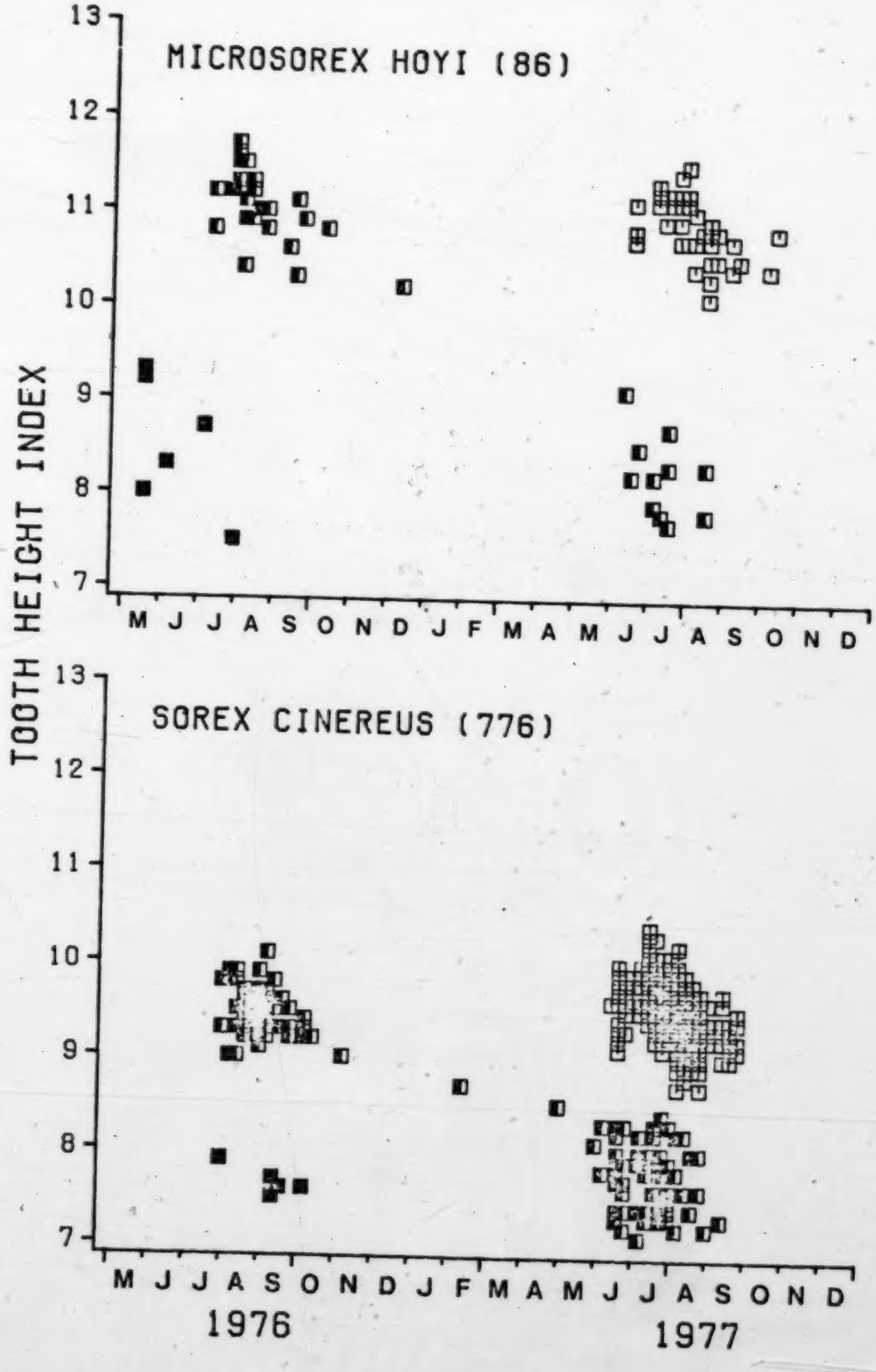
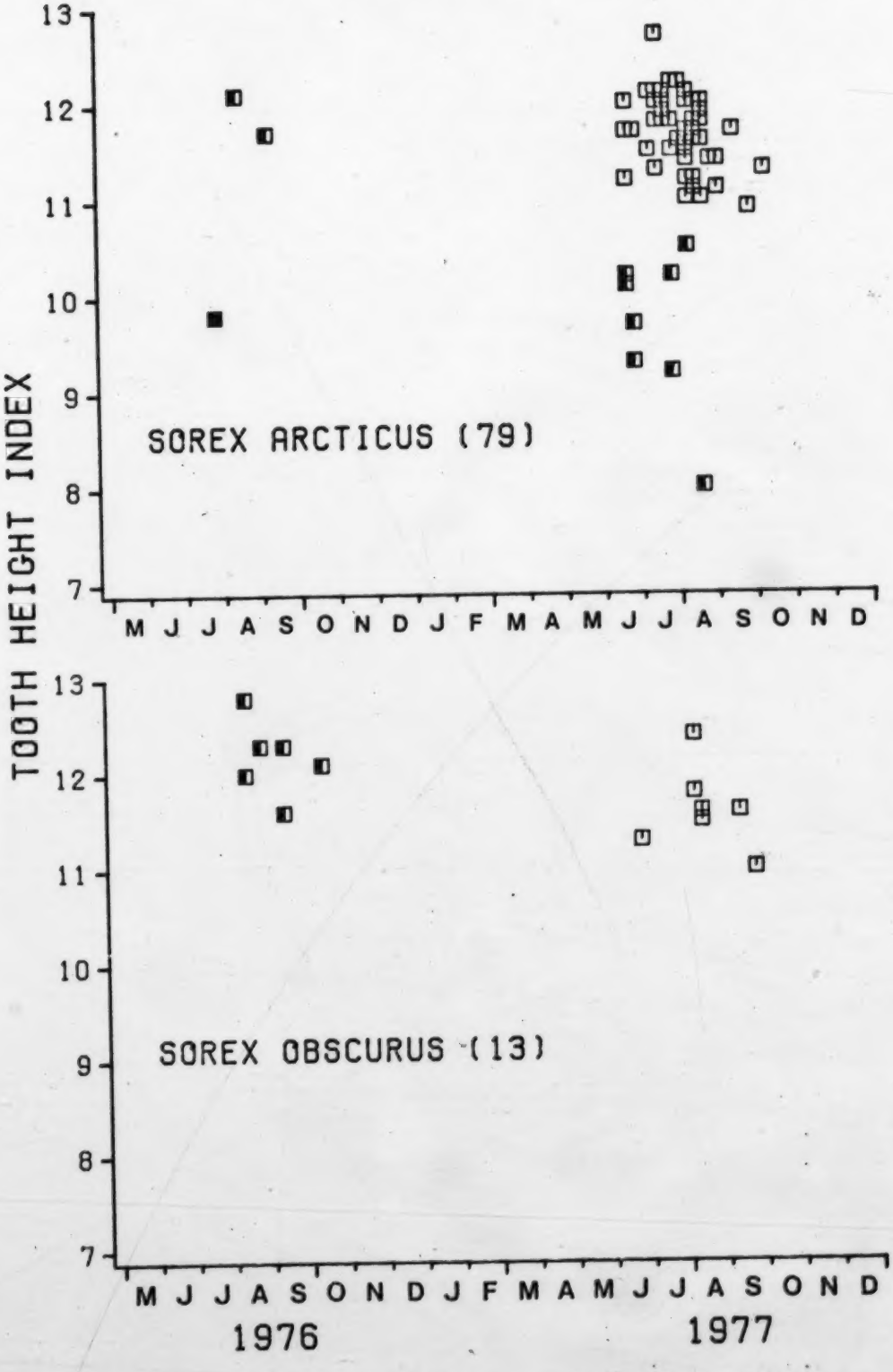

MICROSOREX HOYI (86)
SOREX CINEREUS (776)
TOOTH HEIGHT INDEX
13
12
11
10
9
8
7
M J J A S O N D J F M A M J J A S O N D
1976
1977

Figure 6. Scattergrams of the tooth height indices of S. obscurus and S. arcticus. Three cohorts can be distinguished on the basis of tooth height: 1975 (closed squares), 1976 (half-open squares), and 1977 (open squares). OW animals have lower tooth height values than YY animals. Note that no OW individuals of S. obscurus were caught.


TOOTH HEIGHT INDEX
13
12
11
10
9
8
7
SOREX ARCTICUS (79)
M J J A S O N D J F M A M J J A S O N D
SOREX OBSCURUS (13)
1976
1977

Numbers Of Shrews And Sympatric Small Rodents

Removal grids

A summary of the number of the small mammals captured on the removal grids is given in Table 4.

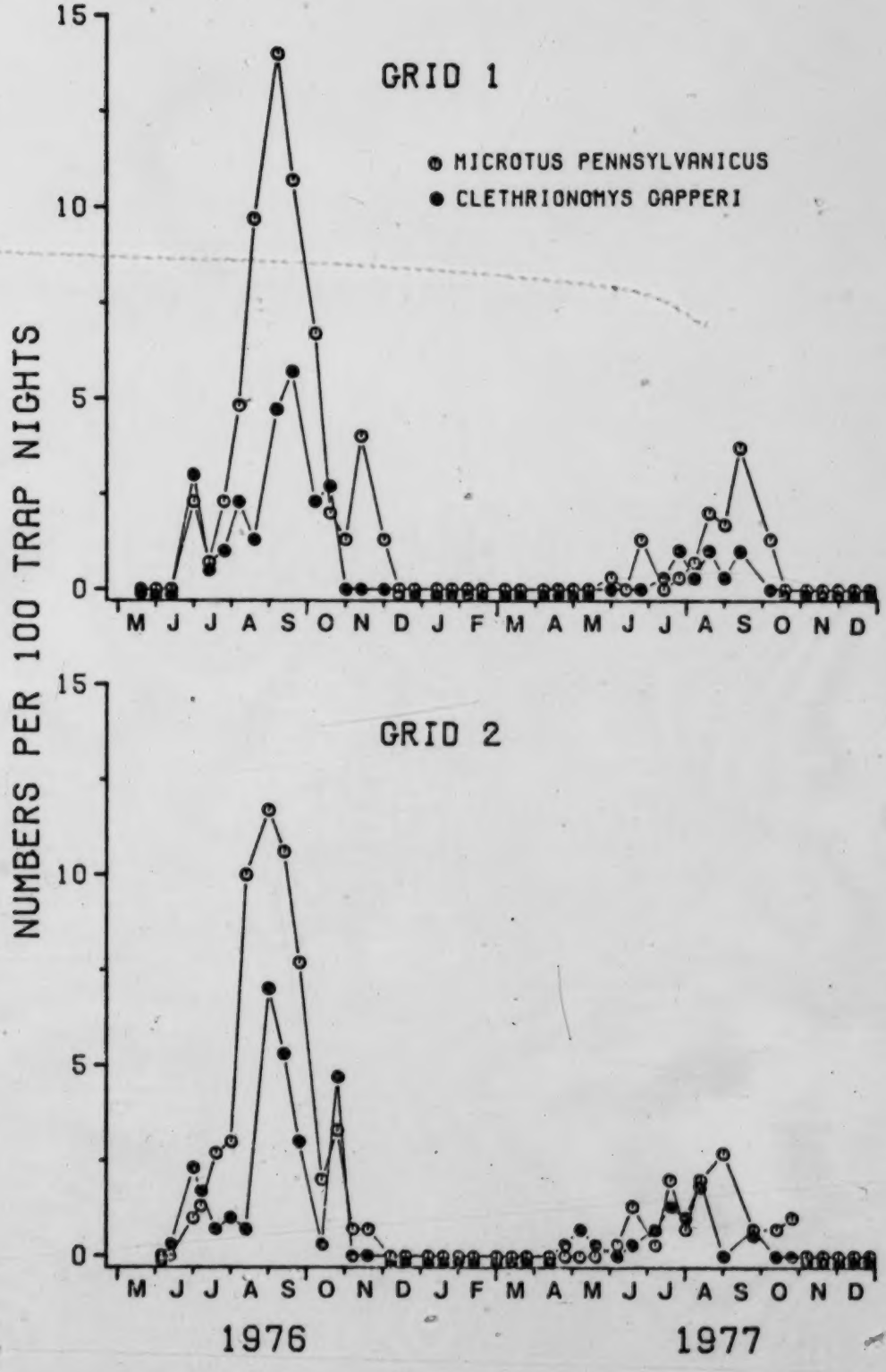
After the small resident populations were removed from the grids in May, 1976, the numbers of animals dispersing onto the grids were followed until December, 1977. Only M. hoyi, M. pennsylvanicus, and C. gapperi were trapped initially, suggesting that other species were in low numbers or absent, and dispersed into the area later.

The dominant rodent species, M. pennsylvanicus and C. gapperi, had high population levels in 1976 but these dropped in 1977 (Fig. 7). The same trend occurred in upland populations of C. gapperi, which are sympatric with P. maniculatus instead of with M. pennsylvanicus. The upland population sampled by snap-trap lines in August of both years declined from 9.2/100 TN to 3.1/100 TN (Fuller, unpublished data), a 66% drop. The lowland population of C. gapperi, based on numbers captured on both grids averaged 5.7/100 TN for 1976 and 1.5/100 TN for 1977. This was a decline of 74%. Thus C. gapperi, though trapped in different habitats and by different methods, showed similar trends in population dynamics.

Table 4. Summary of the number and percentage of small mammals captured on the removal grids from 17 May, 1976 to 28 December, 1977. (TN = trap nights)

Species	1976 (8,050 TN)		1977 (11,550 TN)	
	N	% of total	N	% of total
M. hoyi	29	4.9	22	5.9
S. arcticus	3	0.5	11	2.9
S. cinereus	41	6.9	187	50.0
S. obscurus	6	1.0	3	0.8
Insectivora	79	13.2	223	59.6
C. gapperi	138	23.1	34	9.1
M. pennsylvanicus	325	54.4	68	18.2
P. intermedius	40	6.7	24	6.4
P. maniculatus	4	0.7	9	2.4
S. borealis	6	1.0	16	4.3
Z. hudsonius	5	0.8	0	0.0
Rodentia	518	86.8	151	40.4
Total	597		374	

Figure 7. Changes in numbers of M. pennsylvanicus and C. gapperi on grids 1 and 2.


GRID 1
MICROTUS PENNSYLVANICUS
CLETHRIONOMYS GAPPERI
NUMBERS PER 100 TRAP NIGHTS
15
10
5
0
M J J A S O N D J F M A M J J A S O N D
GRID 2
15
10
5
0
M J J A S O N D J F M A M J J A S O N D
1976
1977

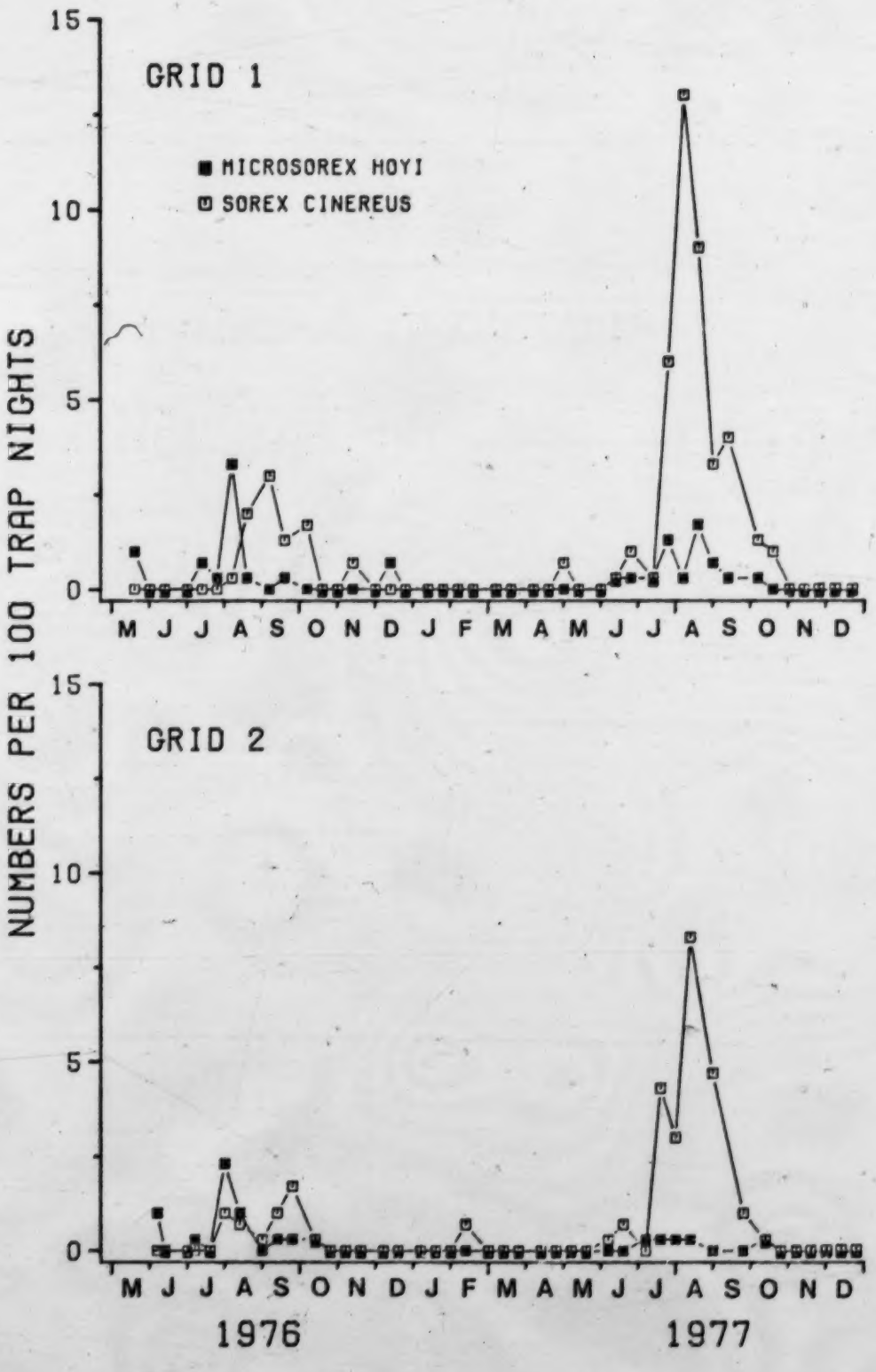
For a 5-month period during winter and early spring no small rodents were taken in the pitfalls though they were present on both grids as indicated by tracks in the snow crossing my trail between the trapping stations.

M. hoyi was initially the only shrew species on the grids with S. cinereus first appearing in early August. S. arcticus and S. obscurus were only caught occasionally. The 1976 populations of M. hoyi and S. cinereus remained low but in 1977, S. cinereus started to increase in mid-July and reached levels as high as those reached by M. pennsylvanicus in the previous year (Fig. 8).

Shrews, like rodents, were almost entirely absent from the traps during the period of snow cover.

The rate of dispersal of small mammals during the summer seemed to be more or less continuous, giving a reliable index to their relative abundance even though trapping on the removal grids was done for three days every two weeks.

Figure 8. Changes in numbers of M. hovi and S. cinereus on grids 1 and 2.


GRID 1
MICROSOREX HOYI
SOREX CINEREUS
NUMBERS PER 100 TRAP NIGHTS
15
10
5
0
M J J A S O N D J F M A M J J A S O N D
GRID 2
15
10
5
0
M J J A S O N D J F M A M J J A S O N D
1976
1977

Pitfall trap lines

A dramatic change in the relative abundance of shrews was apparent after trap lines were shifted to shrub birch fens. Shrews increased in numbers while rodents were essentially absent (Table 5). S. cinereus appeared in large numbers; S. arcticus and M. hoyi appeared consistently at low levels (Fig. 9). The dramatic increase in population numbers after mid-June was partly due to the appearance of YY animals but a comparison with the numbers caught on the grids reveals a very real difference in the relative abundance.

An unusually high local population of S. cinereus was sampled twice in a shrub birch fen along Heart Lake. Their numbers were plotted separately in Figure 9.

The numbers of shrews caught on trap lines in black spruce fens were similar to those caught on the removal grids while the relative abundance index obtained from shrub birch trap lines was consistently higher.

Upland trapping

Intensive and extensive trapping in upland areas by Dr. W.A. Fuller and his students turned up few shrews. Only S. cinereus was taken in any number while only two and four specimens of M. hoyi and S. arcticus were caught, respectively. S. cinereus numbers from snap-trap lines (Table 6) agreed with the observed low numbers in 1976 and

Table 5. Summary of the number and percentage of small mammals captured on the pitfall trap lines in 1977. There was a total of 1700 trap nights.

Species	N	% of total
M. hoyi	26	6.9
S. arcticus	53	14.0
S. cinereus	251	66.4
S. obscurus	1	0.3
Insectivora	331	87.6
C. gapperi	14	3.7
M. pennsylvanicus	18	4.8
P. intermedius	2	0.5
P. maniculatus	1	0.3
S. borealis	10	2.6
Z. hudsonius	1	0.3
Rodentia	46	12.2
Total	378	

Figure 9. Changes in numbers of M. hoyi, S. cinereus, and S. arcticus on pitfall trap lines. Very high numbers of S. cinereus taken locally along Heart Lake are plotted separately (dashed line).

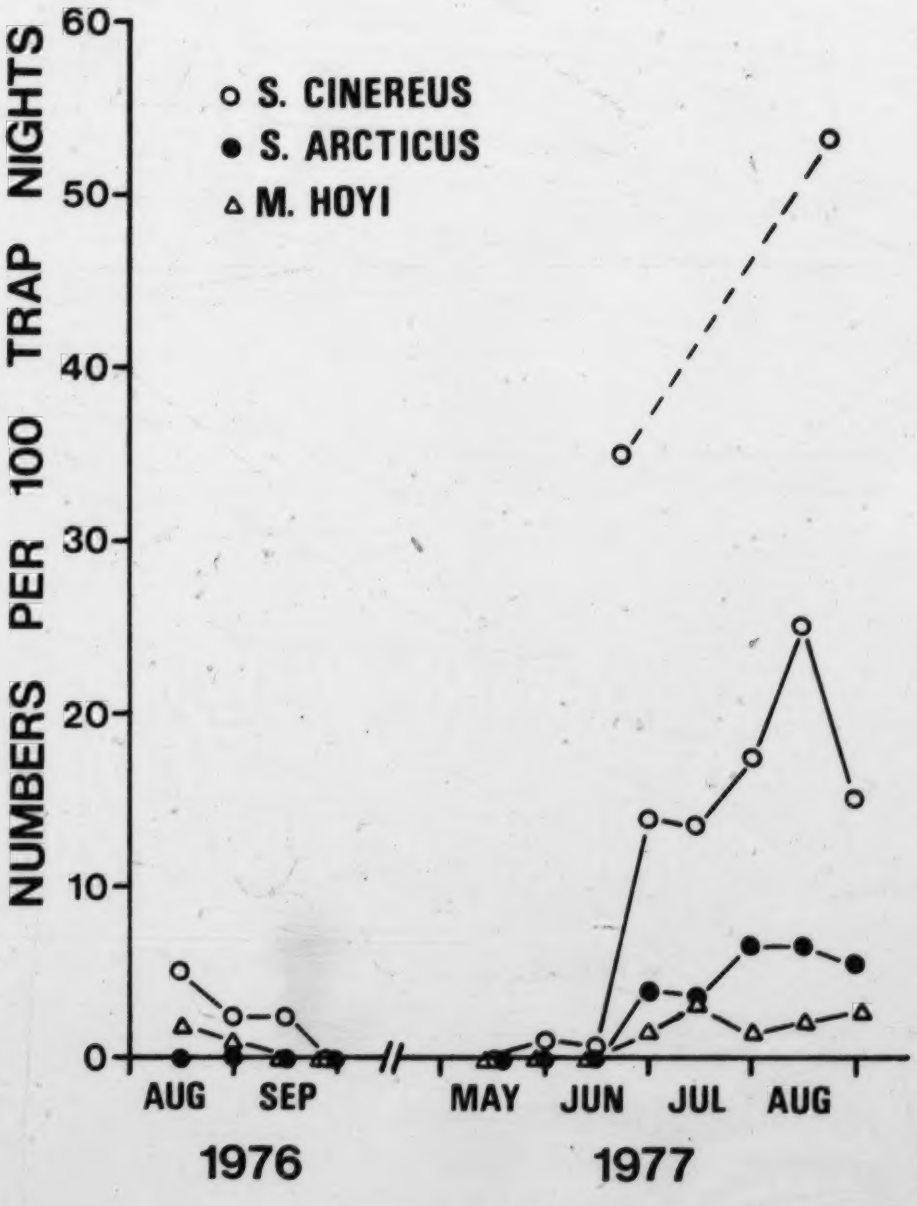

NUMBERS PER 100 TRAP NIGHTS
60
50
40
30
20
10
0
S. CINEREUS
S. ARCTICUS
M. HOYI
AUG
SEP
MAY
JUN
JUL
AUG
1976
1977

Table 6. Upland snap-trapping indices for S. cinereus, 1976-77. (TN = trap nights; C = catch).

Month	TN	C/100 TN
1976		
Aug	2259	0.3
Sep	600	0.2
1977		
Jul	1938	0.7
Aug	2348	2.8

peak in 1977 from the present lowland study.

Reproduction

Males

Histological examination of the testes of male shrews revealed the following:

1. All males with a testis length > 2 mm in *M. hoyi* and *S. cinereus* and > 3 mm in *S. arcticus* had sperm in the seminiferous tubules. These animals were considered to be in breeding condition. They also had a large epididymis with visible tubules and enlarged seminal vesicles.
2. All males with a testis length ≤ 1 mm in *M. hoyi* and *S. cinereus* and ≤ 2 mm in *S. arcticus* had no sperm in the seminiferous tubules. These animals were considered non-breeding. The reproductive system was tiny and difficult to find during the autopsy.

Females

Female shrews of all species were considered to be in breeding condition if they were pregnant, lactating, or in estrus. Animals were judged to be in estrus if the uterus was enlarged and opaque, and the ovaries contained mature follicles.

Previously reproductive females could be recognized by the presence of thick-walled blood vessels in the mucosa of the uterus (Pearson 1944). Placental scars were often present but their sometime absence, as demonstrated by Pearson (1944) in captive Blarina, made the appearance of uterine blood vessels a more reliable indicator of previous breeding.

Breeding phenology

A summary of the total numbers of breeding and non-breeding animals is given in Table 7. Breeding females were caught rarely and late in their reproductive cycle. Therefore the beginning of the breeding season for each species was an estimate based on a 20 day gestation period and 21 days in the nest as demonstrated for S. araneus in Europe (Dehnel 1952).

M. hoyi

A lactating female was captured on 18 May indicating a conception date before 28 April. The first independent YY

Table 7. Total numbers of breeding and non-breeding male and female shrews in 1976 and 1977. (B = breeding, N-B = non-breeding).

Species	Males		Females	
	N-B	B	N-B	B
1976				
M. hoyi	17	5	11	1
S. cinereus	41	4	24	1
S. arcticus	1	1	1	0
S. obscurus	3	0	3	0
1977				
M. hoyi	21	11	15	4
S. cinereus	281	72	292	37
S. arcticus	38	6	26	3
S. obscurus	1	0	4	2

animals were taken on 20 June confirming that the breeding season started in late April or early May.

The only indication of breeding in YY females was one in estrus captured on 20 June in 1977. The number of such females must be small and their contribution to the population negligible.

A pregnant OW female with traces of old placental scars taken on 23 August would indicate that two or possibly three litters could be produced each year.

YY males did not mature in their first year so only OW males were in breeding condition.

S. cinereus

The breeding season started in early May as implied by a lactating female taken on 31 May and YY animals caught on 20 June. OW females gave birth to a second litter in early July. Surviving OW females, few in number, produced a third litter in late August. YY females matured rapidly in 1977 and had a litter in July and a second in August. As with M. hoyi, it was only in 1977 that YY females were observed to mature. Only females from the first litters became sexually mature as indicated by the capture of YY females in estrus only at the end of June. No YY males were observed to mature in their year of birth.

The breeding intensity of S. cinereus was evaluated from 1977 trap line samples from otherwise undisturbed populations (Fig. 10). Breeding male numbers dropped steadily during the summer. The catch of breeding females dropped sharply after mid-July.

S. arcticus

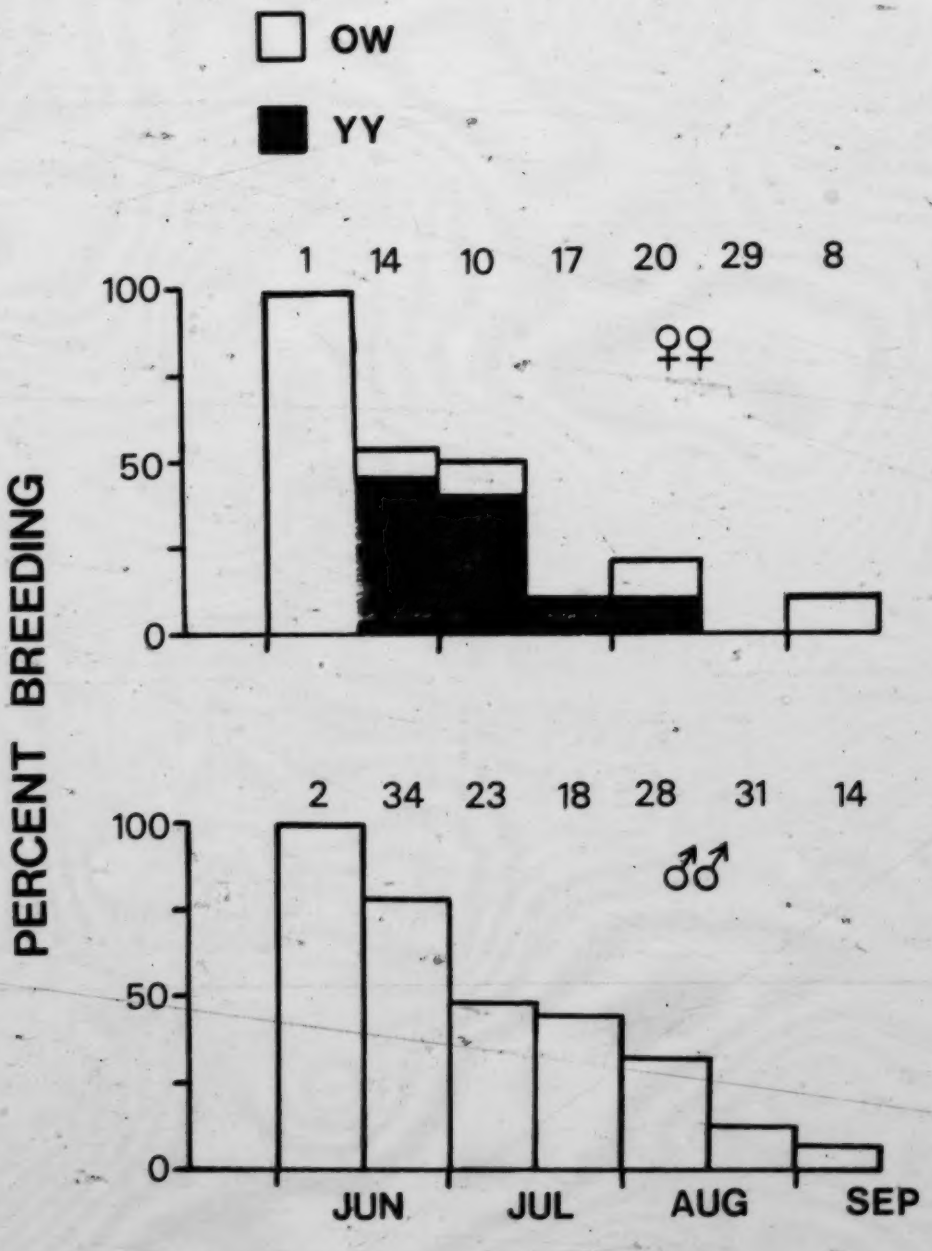
No breeding OW females were taken until late July but YY animals caught on 20 June indicate that the breeding season started in early May. Pregnant YY females were taken in late June, 1977. The last pregnant OW female was captured on 11 August, which indicates that two or three litters per year are possible.

S. obscurus

From the scant data collected, it would seem that S. obscurus has a breeding phenology similar to the other species. The first YY animal captured on 29 June, 1977 was a female in estrus; another female was taken in mid-August that was pregnant. It was only in 1977 that breeding YY females were caught, while YY males were not observed to mature sexually either year.

All four species of shrews seem to have a similar breeding phenology. The breeding season extends from late April or early May to late August. OW females produce two, possibly three litters per year. The YY females from first

Figure 10. Breeding intensity in S. cinereus from 1977 pitfall trap line data. The number above the bars is the sample size. The shaded portion of each bar represents the proportion of breeding YY females.


OW
YY
1 14 10 17 20 29 8
♀♀
100
50
0
PERCENT BREEDING
2 34 23 18 28 31 14
♂♂
100
50
0
JUN
JUL
AUG
SEP

litters matured rapidly in 1977 but failed to mature in 1976. In 1977, YY females of all species were capable of producing at least one litter with S. cinereus YY females having a second. Only OW males matured to breed throughout the summer.

Litter size

Litter sizes, estimated from placental scar counts, embryos, and a combination of both, were similar for M. hoyi, S. cinereus and S. arcticus (Table 8). Only one female S. obscurus was caught from which a litter size could be determined; it was pregnant with six embryos. Placental scars were counted only when they were distinct.

The mean litter size (8.82 ± 0.44) of 11 OW female S. cinereus was significantly ($p = 0.01$) greater than the mean litter size (7.59 ± 0.87) of 17 YY females.

Table 8. 1976-77 litter size estimates for *M. hoyi*, *S. cinereus*, and *S. arcticus* OW and YY females. (Mean ± SE; n is in parentheses).

Species	Litter size		
	Scars	Embryos	Combined
M. hoyi	8.50 ± 1.50 (2)	8.00 (1)	8.33 ± 0.88 (3)
S. cinereus	8.04 ± 0.25 (24)	8.25 ± 0.85 (4)	8.07 ± 0.24 (28)
S. arcticus	----	8.25 ± 0.48 (4)	8.25 ± 0.48 (4)

Population Structure

Sex ratio

The YY animals showed no significant deviations from the expected 1:1 sex ratio (Table 9). In M. hoyi, S. cinereus, and S. arcticus, males comprised a very large propertion of the OW animals caught. This was significantly different frcm the expected ratio for M. hoyi and S. cinereus. The large numbers of OW males caught explain the overall predominance of males for each species. The overall sex ratio differed significantly only for M. hoyi. The large number of M. hoyi OW males and small sample of YY animals caused the shift in the sex ratio.

The large number of OW males caught in pitfalls is probably the result of their range expansion during the breeding season (Shillito 1963; Michielsen 1966; Hawes 1977; and others).

Effect of habitat and dispersal

The effect of habitat and dispersal on population structure of shrews is discussed separately for M. hoyi, S. cinereus, and S. arcticus. The small number of YY S. obscurus caught were from the removal grids, indicating that dispersal occurred even though their population numbers were low, and their distribution was limited.

Table 9. Testing for 1:1 sex ratio in *M. hovi*, *S. arcticus*, *S. cinereus*, and *S. obscurus* (M = males).

Age groups	M	%M	N	X^2
M. hovi				
OW	16	80.0	20	7.20 **
YY	38	58.5	65	1.86
Total	54	63.5	85	6.22 *
S. arcticus				
OW	7	70.0	10	1.60
YY	39	56.5	69	1.17
Total	46	58.2	79	2.14
S. cinereus				
OW	76	84.4	90	42.71 ***
YY	321	48.9	657	0.34
Total	397	53.1	747	2.96
S. obscurus				
OW	--	--	--	--
YY	4	30.8	13	1.92
Total	4	30.8	13	1.92

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

S. cinereus

Table 10 summarizes the population structure of S. cinereus in lowlands (trap lines), uplands, and on the removal grids. The population structure was dependent on the sampling location as indicated by the significant chi-square.

The population structure of samples taken from trap lines were significantly different from samples taken from removal grids ($X^2 = 47.89$, $p < 0.001$) and uplands ($X^2 = 41.46$, $p < 0.001$).

In lowland areas breeding animals comprised 27.6% of the population as compared to 5.3% and 6.0% for the grids and uplands, respectively. Non-breeding YY animals made up 94.7% and 94.0% of animals taken on grids and uplands, respectively, but only 72.4% of those taken in the lowlands. The S. cinereus population structure in uplands was similar to that found on the removal grids ($X^2 = 5.31$, n.s.), suggesting dispersal from shrub birch fens into both of these areas. The high number of immature YY animals and the lack of breeders support this interpretation.

M. hoyi

Only two M. hoyi were ever captured in upland areas indicating that its populations were essentially confined to lowland areas (Table 11). Although the trend suggests

Table 10. Comparison of the population structure of *S. cinereus* in three different sampling locations. Percentages are in parentheses. (OW = overwintered, YY = young of the year, N-B = non-breeding, B = breeding, M = males, F = females).

Location	OW M	OW F	YY M	N-B YY F	B YY F	Total
Removal grids	7 (3.1)	3 (1.3)	98 (43.4)	116 (51.3)	2 (0.9)	226
Lowland (Trap lines)	61 (19.8)	8 (2.6)	121 (39.3)	102 (33.1)	16 (5.2)	308
Upland	3 (1.5)	3 (1.5)	98 (49.0)	90 (45.0)	6 (3.0)	200

$X^2 = 78.97$, $p < 0.001$

dispersal from shrub birch to wooded fens, the chi-square is not significant. Though trap line samples tend to have greater proportions of OW animals (32.3%) and a smaller proportion of YY animals (67.7%) than the removal grids, 18.0% and 82.0%, respectively, these differences are also not significant ($X^2 = 2.17$, n.s.).

S. arcticus

As with M. hoyi, S. arcticus was essentially absent from the upland; only four YY animals were caught. Table 12 summarizes the population structure in lowland areas. The population structure seemed to be independent of the location and tended to be similar between the removal grids and trap lines. The small number of animals caught on the removal grids and in upland areas suggests that dispersal was minimal.

Table 11. Comparison of the population structure of *M. hoyi* in the lowland areas. Percentages are in parentheses. (OW = overwintered; YY = young of the year, M = males, F = females).

Location	OW M	OW F	YY M	YY F	Total
Removal grids	7 (14.0)	2 (4.0)	23 (46.0)	18 (36.0)	50
Trap lines	8 (25.8)	2 (6.5)	12 (38.7)	9 (29.0)	31

$X^2 = 2.19$, $p = 0.53$

Table 12. Comparison of the population structure of S. arcticus in the lowland areas. Percentages are in parentheses. (OW = overwintered; YY = young of the year, M = males, F = females).

Location	OW	YY M	YY F	Total
Removal grids	3 (21.4)	6 (42.9)	5 (35.7)	14
Trap lines	6 (10.0)	32 (53.3)	22 (36.7)	60

$X^2 = 1.46$, $p = 0.48$

Body Size

Both weight and length (total length minus tail length) were used as indices of body size. The body sizes of the four shrew species are compared in Table 13. No distinction was made between different sexes or age groups in this preliminary analysis. All the differences were significant except for the mean weights of M. hoyi and S. cinereus.

Except for S. obscurus, for which no OW animals were caught, it was possible to compare different sex and age groups as well. In S. cinereus it was also possible to separate YY females into breeders and non-breeders.

Age group variations

For all species the OW animals were significantly heavier than YY animals, but only in S. cinereus was a significant difference detected between the sexes in equivalent age groups (Table 14). The differences between OW males, OW females, breeding YY females, and non-breeding YY were significant.

Overwintered animals had greater body lengths than YY animals and OW females were longer than OW males for all species (Table 15). In S. cinereus each category was significantly different from every other category.

All these differences suggests that sexual dimorphism may occur in shrews, with the females being the larger sex. In S. cinereus OW females are 7.3% longer and 8.7% heavier

Table 13. Body size comparison of *M. hoyi*, *S. cinereus*, *S. obscurus*, and *arcticus* from the Heart Lake area, N.W.T. Means joined by the same vertical line do not differ at the $p < 0.05$ level of significance (Duncan's multiple range test).

Species	N	Mean ± SE	Range
		Weight (g)	
M. hoyi	84	3.4 ± 0.08	2.4 - 6.0
S. cinereus	714	3.3 ± 0.02	2.2 - 7.1
S. obscurus	13	5.1 ± 0.15	4.2 - 6.2
S. arcticus	74	7.0 ± 0.13	4.6 - 10.4
		Body length (mm)	
M. hoyi	82	57.7 ± 0.35	49.0 - 67.0
S. cinereus	667	55.6 ± 0.09	48.0 - 69.0
S. obscurus	13	64.4 ± 0.68	60.0 - 69.0
S. arcticus	76	69.5 ± 0.38	63.0 - 82.0

Table 14. Weights of *M. hoyi*, *S. arcticus*, and *S. cinereus* from the Heart Lake area, N.W.T. Means joined by the same vertical line do not differ at the $p < 0.05$ level of significance (Duncan's multiple range test).

Age groups	N	Weight (g) Mean ± SE	Range
M. hoyi			
OW M	15	4.6 ± 0.16	3.6 - 6.0
OW F	4	4.2 ± 0.31	3.7 - 5.1
YY M	38	3.1 ± 0.05	2.5 - 3.7
YY F	26	3.2 ± 0.08	2.4 - 4.2
S. arcticus			
OW M	7	9.1 ± 0.35	7.7 - 10.4
OW F	3	8.6 ± 0.50	7.9 - 9.6
YY M	37	6.7 ± 0.12	4.6 - 8.2
YY F	27	6.6 ± 0.15	5.5 - 9.1
S. cinereus			
OW M	64	4.6 ± 0.07	3.5 - 5.8
OW F	12	5.0 ± 0.31	3.6 - 7.1
B YY F	22	3.9 ± 0.13	3.0 - 5.7
YY M	304	3.2 ± 0.02	2.2 - 4.6
N-B YY F	303	3.2 ± 0.02	2.3 - 4.2

Table 15. Body lengths of M. hoyi, S. arcticus, and S. cinereus from the Heart Lake area, N.W.T. Means joined by the same vertical line do not differ at the $p < 0.05$ level of significance (Duncan's multiple range test).

Age groups	N	Body length (mm) Mean ± SE	Range
M. hoyi			
OW M	15	61.1 ± 0.56	57 - 64
OW F	4	63.7 ± 1.38	61 - 67
YY M	36	56.2 ± 0.36	51 - 60
YY F	26	56.8 ± 0.50	49 - 60
S. arcticus			
OW M	7	73.9 ± 1.75	66 - 80
OW F	3	78.3 ± 1.86	76 - 82
YY M	37	68.9 ± 0.35	63 - 72
YY F	29	68.5 ± 0.35	65 - 72
S. cinereus			
OW M	64	59.2 ± 0.30	54 - 64
OW F	11	63.5 ± 0.94	57 - 69
B YY F	21	57.0 ± 0.62	52 - 66
YY M	282	54.8 ± 0.10	48 - 59
N-B YY F	283	55.3 ± 0.09	50 - 63

than the OW males. S. arcticus and M. hoyi OW females are significantly longer but tend to be lighter though the difference in weight is not significant.

Seasonal variations

Seasonal variations in body size were studied by comparing all individuals of the same cohort. Significant differences between sexes of the same cohort do occur as shown above but these differences are not as great as those caused by lumping all individuals (YY and OW) of a species caught during a particular period together. Animals from each species, except S. obscurus, were divided into three cohorts on the basis of tooth height and year of capture. Small sample sizes for most months made it necessary to use season as the time period examined. Winter was considered to be November to April, inclusive. Summer consisted of July and August which were analyzed by month because of the large sample sizes. September and October constituted the fall period. Each cohort was considered separately and seasonal means were compared by Duncan's multiple range test.

1975 cohort

There was a tendency for body length of M. hoyi and S. cinereus to decrease with increasing age (Fig. 11), but it was not significant ($p > 0.05$, Duncan's multiple range test), and weight varied nonsignificantly, probably because sample sizes were small. S. arcticus was represented by only one individual.

1976 cohort

This cohort was studied in its entirety: from summer, 1976 as YY animals, to fall, 1977 as OW animals by which time there were few survivors.

Body lengths of M. hoyi and S. cinereus samples (Fig. 11) decreased throughout their first summer into winter and increased significantly in spring (Table 16) when they came into breeding condition. Length continued to increase until August, but dropped significantly in fall (September-October) for S. cinereus, the only species with a fall sample. S. arcticus showed trends in body length similar to M. hoyi and S. cinereus but no winter drop in length was evident because of the small sample size of YY animals.

Body weights showed a winter decrease and spring increase similar to length for M. hoyi and S. cinereus (Fig. 12). The spring jump in weight was significant (Table 17) but instead of increasing with length, summer mean weights decreased significantly from spring means. The fall weight

Figure 11. Seasonal variation in body length of S. arcticus, S. cinereus, and M. hoyi. Three cohorts are presented: 1975 (closed circles), 1976 (open circles), and 1977 (closed squares). For each period the mean (horizontal line) ± SE (box), range (vertical line), and sample size (number above symbol) are given. Standard errors are shown only if they extend beyond the cohort symbols and the sample size is > 3.

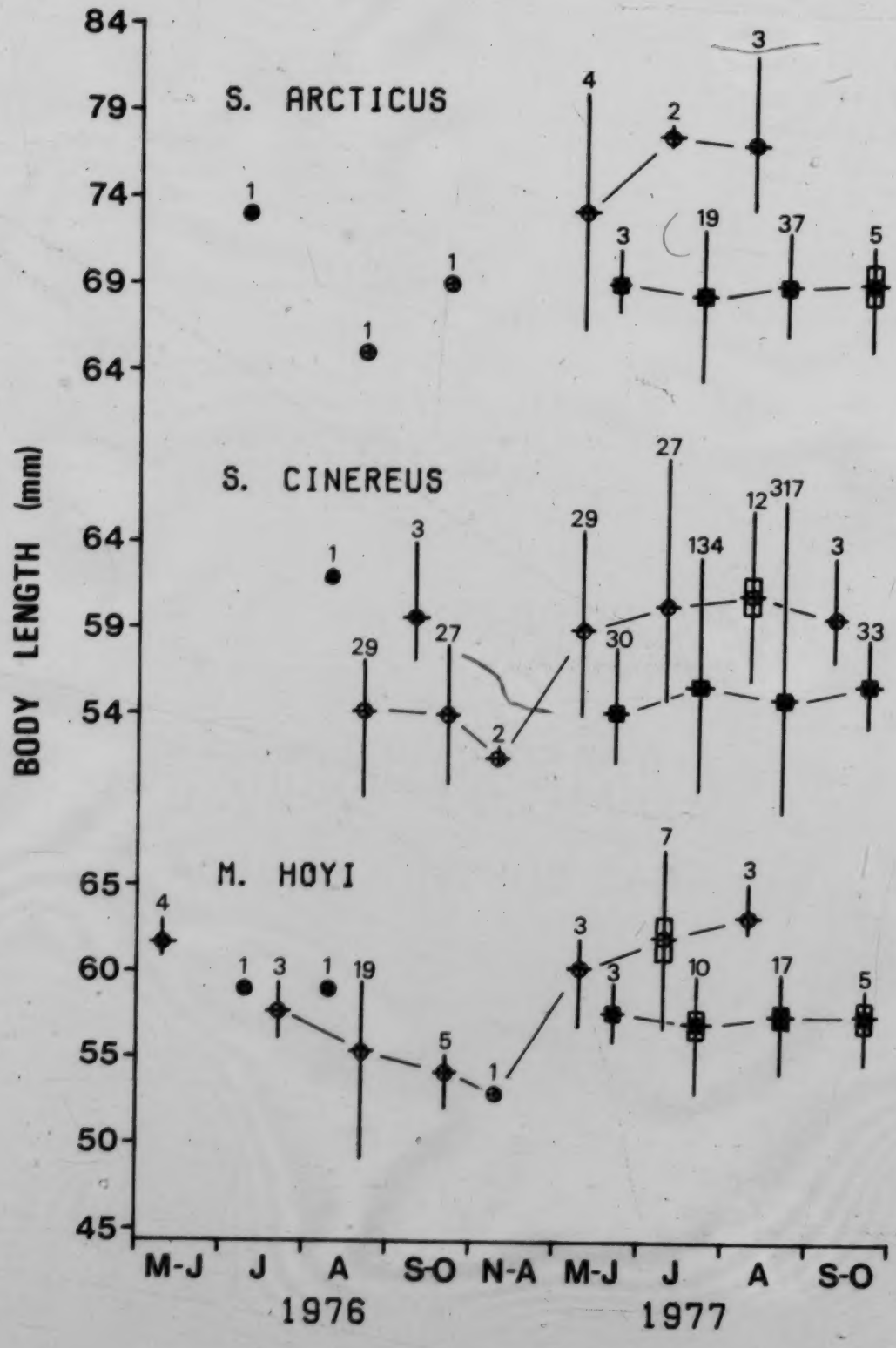

S. ARCTICUS
S. CINEREUS
M. HOYI
BODY LENGTH (mm)
84
79
74
69
64
59
54
65
60
55
50
45
M-J
J
A
S-O
N-A
M-J
J
A
S-O
1976
1977

Table 16. Significance of differences in the body length of the 1976 cohort of *M. hoyi*, *S. cinereus*, and *S. arcticus*. Means joined by the same horizontal line do not differ at the $p < 0.05$ level of significance (Duncan's multiple range test).

Species	Mean body length					
M. hoyi	53.00 Nov-Apr/77	54.20 Sep-Oct/76	55.37 Aug/76	57.70 Jul/76	60.33 May-Jun/77	62.14 Jul/77	63.33 Aug/77
S. cinereus	51.50 Nov-Apr/77	54.04 Sep-Oct/76	54.24 Aug/76	58.89 May-Jun/77	59.67 Sep/77	60.37 Jul/77	61.00 Aug/77
S. arcticus	65.00 Jul/76	69.00 Sep-Oct/76	73.25 May-Jun/77	77.00 Aug/77	77.00 Jul/77		

Figure 12. Seasonal variation in body weight of S. arcticus, S. cinereus, and M. hoyi. Three cohorts are presented: 1975 (closed circles), 1976 (open circles), and 1977 (closed squares). For each period the mean (horizontal line) ± SE (box), range (vertical line), and sample size (number above symbol) are given. Standard errors are shown only if they extend beyond the cohort symbols and the sample size is > 3.

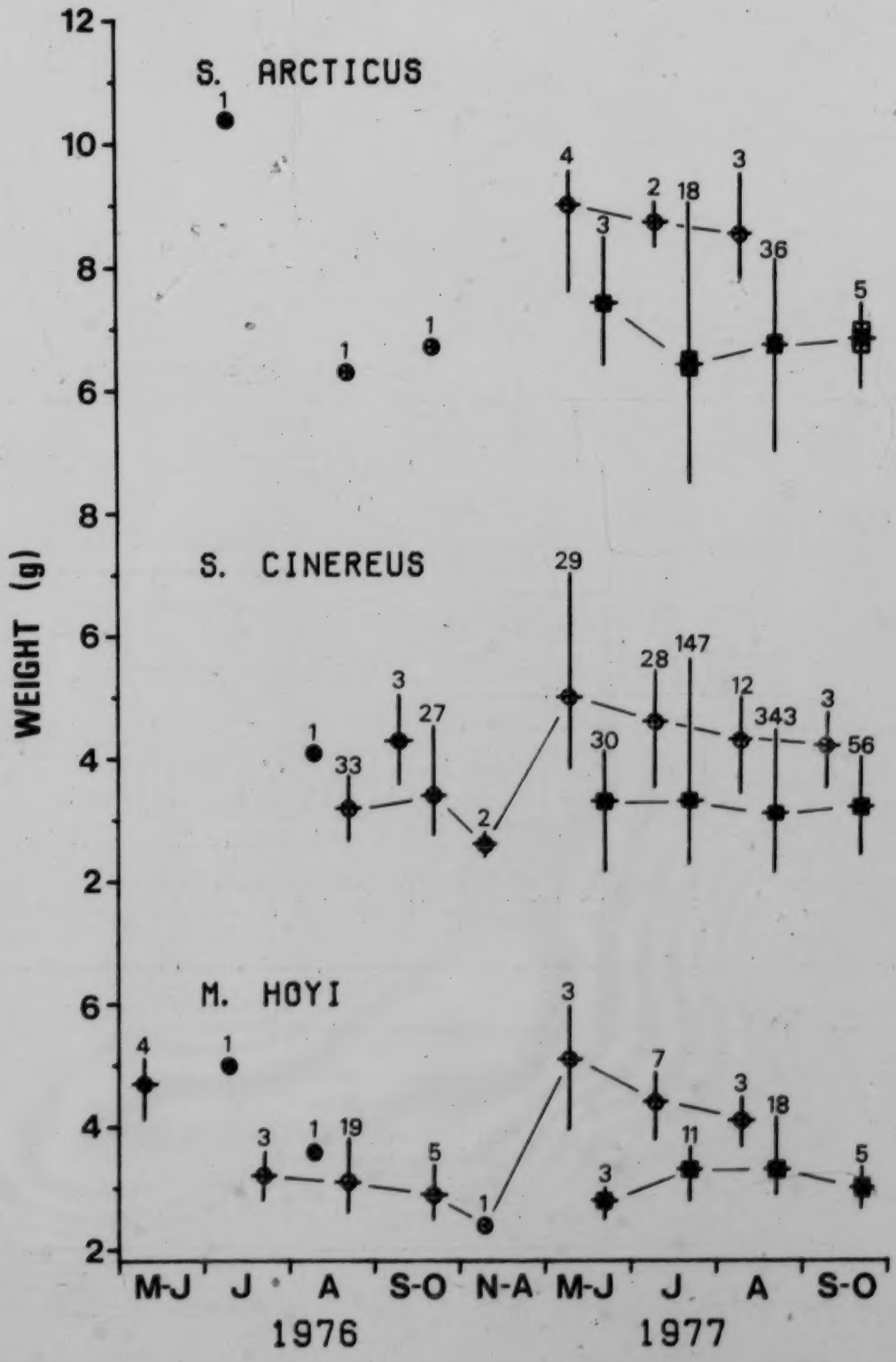

S. ARCTICUS
S. CINEREUS
M. HOYI
WEIGHT (g)
12
10
8
6
4
2
M-J
J
A
S-O
N-A
M-J
J
A
S-O
1976
1977

Table 17. Significance of differences in the body length of the 1976 cohort of M. hoyi, S. cinereus, and S. arcticus. Means joined by the same horizontal line do not differ at the $p < 0.05$ level of significance (Duncan's multiple range test).

Species	Mean body weight						
M. hoyi	2.40 Nov-Apr/77	2.86 Sep-Oct/76	3.13 Aug/76	3.20 Jul/76	4.07 Aug/77	4.37 Jul/77	5.07 May-Jun/77
S. cinereus	2.60 Nov-Apr/77	3.23 Aug/76	3.44 Sep-Oct/76	4.17 Sep/77	4.27 Aug/77	4.57 Jul/77	5.01 May-Jun/77
S. arcticus	6.30 Aug/76	6.70 Sep-Oct/77	8.50 Aug/77	8.75 Jul/77	9.00 May-Jun/77		

of S. cinereus continued the trend in weight loss but was not significantly different from the summer means. S. arcticus showed trends in weight similar to M. hoyi and S. cinereus but again the winter decrease was missing as a result of the small sample. The spring mean weight was significantly greater than the August mean.

1977 cohort

Body length and weight of these YY animals tended to remain constant during the snow-free period (Figs. 11, 12), but there were some significant differences (Table 18).

M. hoyi showed no change in length but significantly increased in weight during the summer months from spring, only to drop back in the fall to a level similar to the spring mean.

Both weight and length of S. cinereus dropped significantly between July and August but recovered in the fall. This drop in body size was probably caused by a large influx of newly weaned young into the trappable population. Peak summer numbers also occurred in this period presumably as a result of that influx. No significant changes occurred in the body size of S. arcticus though weight showed some variation.

Table 18. Significance of differences in the body size of the 1977 cohort of *M. hoyi*, *S. cinereus*, and *S. arcticus*. Periods joined by the same horizontal line do not differ at the $p < 0.05$ level of significance (Duncan's multiple range test).

Body size	Mean of periods			
Weight				
M. hoyi	2.80 May-Jun	2.96 Sep-Oct	3.28 Jul	3.31 Aug
S. cinereus	3.10 Aug	3.22 Sep-Oct	3.28 Jul	3.29 May-Jun
S. arcticus	6.44 Jul	6.69 Aug	6.82 Sep-Oct	7.40 May-Jun
Length				
M. hoyi	57.10 Jul	57.60 Sep-Oct	57.65 Aug	57.67 May-Jun
S. cinereus	54.23 May-Jun	55.00 Aug	55.73 Jul	55.81 Sep-Oct
S. arcticus	68.32 Jul	68.92 Aug	69.00 Sep-Oct	69.00 May-Jun

Cranial Height

Cranial height, like body size, was analyzed according to age groups and season. For all species, OW animals have lower mean cranial heights than YY animals. This difference was not significant for M. hoyi but was for S. cinereus and S. arcticus males and females (Table 19). Again the animals of each species, except S. obscurus, were divided into three cohorts and comparisons were made by means of Duncan's multiple range test.

1975 cohort

The cranial heights of M. hoyi and S. cinereus showed some variation (Fig. 13), but there were no significant differences ($p > 0.05$, Duncan's multiple range test). There was only one S. arcticus in this cohort.

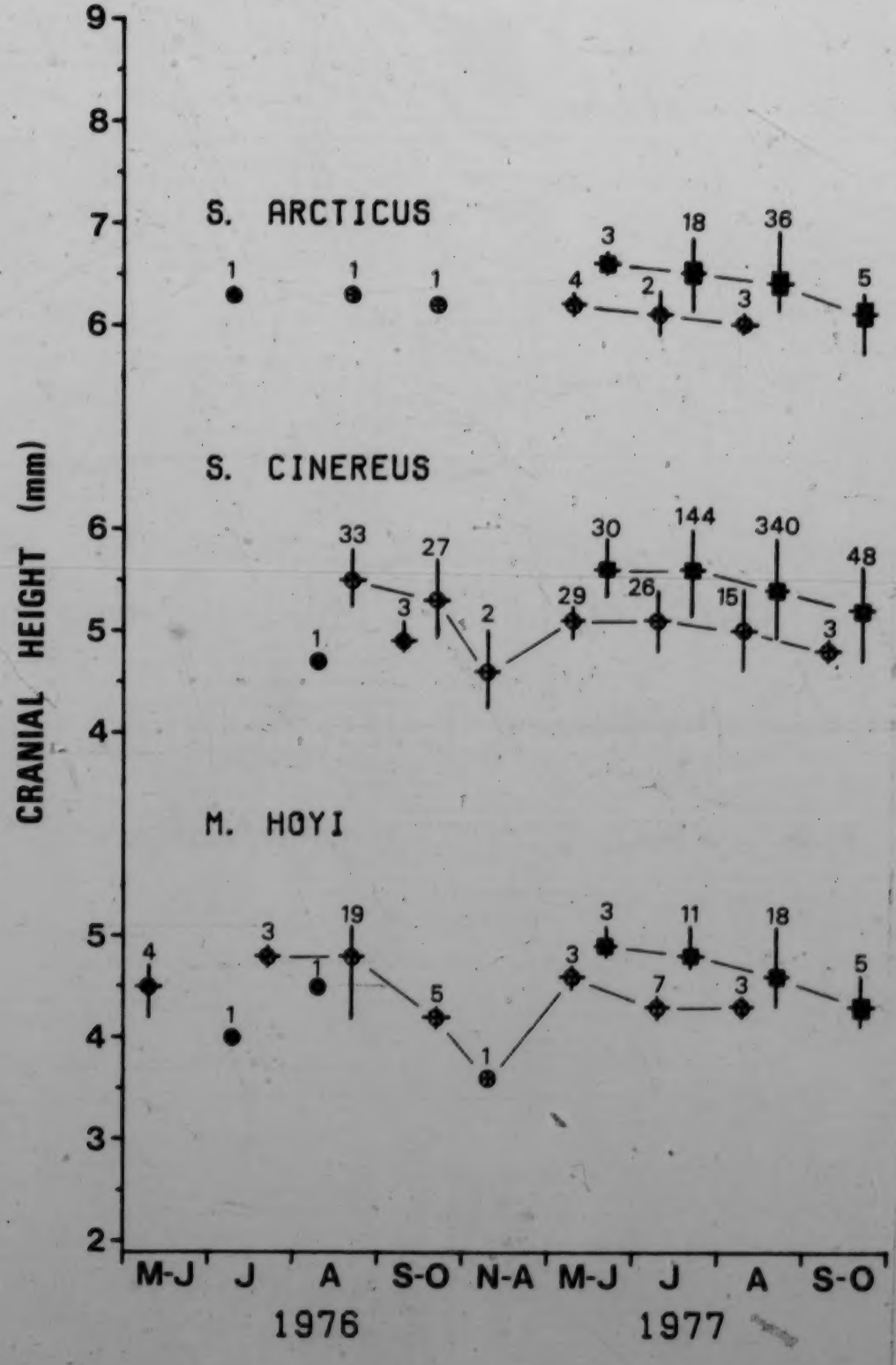
1976 cohort

The seasonal trends in cranial height were similar for M. hoyi and S. cinereus (Fig. 13). There was a significant decrease to a winter low followed by a significant spring increase to a summer level lower than that of the previous summer (Table 20). It was also possible, for S. cinereus only, to show that the mean fall cranial height was significantly lower than the August mean in both 1976 and 1977. No significant seasonal differences appeared in the small samples of S. arcticus.

Table 19. Cranial heights of M. hoyi, S. arcticus, and S. cinereus from the Heart Lake area, N.W.T. Means joined by the same vertical line do not differ at the $p < 0.05$ level of significance (Duncan's multiple range test).

Age groups	N	Cranial height (mm) Mean ± SE	Range
M. hoyi			
OW M	15	4.40 ± 0.05	4.0 - 4.7
OW F	4	4.35 ± 0.12	4.2 - 4.7
YY M	38	4.64 ± 0.04	4.2 - 5.1
YY F	26	4.65 ± 0.07	3.6 - 5.1
S. arcticus			
OW F	3	5.97 ± 0.03	5.9 - 6.0
OW M	7	6.21 ± 0.03	6.1 - 6.3
YY F	27	6.35 ± 0.04	6.1 - 6.9
YY M	39	6.42 ± 0.04	5.7 - 6.8
S. cinereus			
OW M	64	5.06 ± 0.02	4.7 - 5.4
OW F	13	4.97 ± 0.05	4.6 - 5.3
YY M	297	5.46 ± 0.01	4.2 - 5.9
N-B YY F	296	5.41 ± 0.01	4.8 - 6.0
B YY F	21	5.40 ± 0.05	5.1 - 5.8

Figure 13. Seasonal variation in cranial height of S. arcticus, S. cinereus, and M. hoyi. Three cohorts are presented: 1975 (closed circles), 1976 (open circles), and 1977 (closed squares). For each period the mean (horizontal line) ± SE (box), range (vertical line), and sample size (number above symbol) are given. Standard errors are shown only if they extend beyond the cohort symbols and the sample size is > 3.


CRANIAL HEIGHT (mm)
S. ARCTICUS
S. CINEREUS
M. HOYI
M-J
J
A
S-O
N-A
M-J
J
A
S-O
1976
1977

2 2

OF/DE

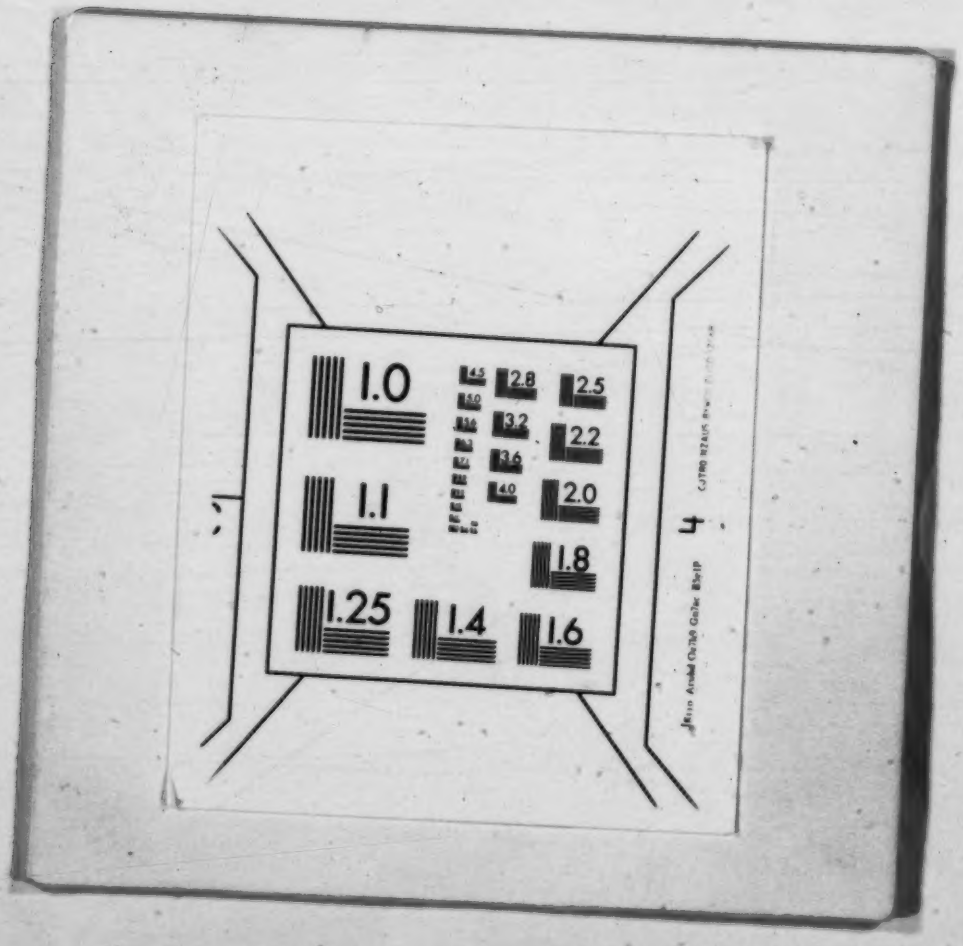


Table 20. Significance of differences in the body length of the 1976 cohort of *M. hoyi*, *S. cinereus*, and *S. arcticus*. Means joined by the same horizontal line do not differ at the $p < 0.05$ level of significance (Duncan's multiple range test).

Species	Mean cranial height					
M. hoyi						
3.60 Nov-Apr/77	4.24 Sep-Oct/76	4.27 Aug/77	4.34 Jul/77	4.60 May-Jun/77	4.77 Aug/76	4.83 Jul/76
S. cinereus						
4.60 Nov-Apr/77	4.83 Sep/77	5.05 Aug/77	5.06 Jul/77	5.08 May-Jun/77	5.33 Sep-Oct/76	5.55 Aug/76
S. arcticus						
6.03 Aug/77	6.10 Jul/77	6.20 Sep-Oct/76	6.20 May-Jun/77	6.30 Aug/76		

1977 cohort

The cranial height in all three species decreased from spring to fall (Fig. 13). Spring and July heights in all the species were not significantly different (Table 21). For all three species August and fall means were significantly different from each other and from both spring and July means.

Microhabitat

The frequency of capture of M. hoyi, S. cinereus, and S. arcticus in each of four microhabitats on the removal grids was analyzed (Table 22). The analysis revealed that M. hoyi and S. cinereus were caught more frequently than expected in moist areas, both open and closed. Both species were caught less frequently than expected in dry microhabitats. The number of S. arcticus caught in each microhabitat was similar to the expected proportions as determined by the number of trapping stations in each of the microhabitats described. These results are interpreted as preference for or avoidance of certain microhabitats by shrew species. M. hoyi and S. cinereus seemed to prefer moist areas whether open or closed, while they avoided dry areas. S. arcticus had similar preferences but seemed to be able to tolerate dry areas better than the two smaller species.

Table 21. Significance of differences in the cranial height of the 1977 cohort of *M. hoyi*, *S. cinereus*, and *S. arcticus*. Means joined by the same horizontal line do not differ at the $p < 0.05$ level of significance (Duncan's multiple range test).

Species	Mean cranial height			
M. hoyi	4.30	4.58	4.80	4.90
	Sep-Oct	Aug	Jul	May-Jun
S. cinereus	5.17	5.40	5.56	5.62
	Sep-Oct	Aug	Jul	May-Jun
S. arcticus	6.12	6.37	6.49	6.63
	Sep-Oct	Aug	Jul	May-Jun

Table 22. Analysis of capture frequencies of *M. hoyi*, *S. cinereus*, and *S. arcticus* from 200 trapping stations in four microhabitats on the removal grids. The proportion of the total is in parentheses.

Statistics	N	Microhabitats: Open Dry	Open Wet	Closed Dry	Closed Wet	X^2
Expected		44 (.22)	73 (.36)	25 (.12)	58 (.29)	
Observed						
M. hoyi	51	2 (.04)	26 (.51)	0 (.00)	23 (.45)	21.36*
S. cinereus	226	27 (.12)	89 (.39)	21 (.09)	89 (.39)	21.20*
S. arcticus	14	3 (.21)	6 (.43)	1 (.07)	4 (.29)	0.49

*$p < 0.005$

These results are somewhat general, as a trapping station was included in a particular microhabitat on the basis of its location. The immediate microenvironment surrounding each pitfall is probably more important than its general location in determining the number of shrews caught, so a detailed analysis of vegetational cover was done at each of the 200 pitfalls on the removal grids.

Effect of cover

The interrelationships of shrew abundance (dependent variable) and classes of tree, shrub, herb, graminoid, moss, and lichen cover were analyzed by means of analysis of variance and MCA. Moss and tree cover contributed little to the explanation of variance so both were omitted from the final analysis. Some of the cover classes had to be combined so there would be enough cases for analysis. The dependent variable was transformed to $\sqrt{x + 0.5}$ as suggested by Sokal and Rohlf (1969) for count data including zero values.

The results of the analyses of variance are summarized in Table 23. There were significant differences in the abundance of M. hoyi with lichen and herb cover, S. cinereus with herb and shrub cover, and S. arcticus with lichen cover. Though significant, these results do not provide any information about the pattern of the effects, therefore, these data were further analyzed by MCA.

Table 23. Results of the analyses of variance of the abundance of three shrew species on the removal grids in relation to vegetational cover. (df = degrees of freedom)

Source of variation	*M. hoyi*		*S. cinereus*		*S. arcticus*	
	df	F	df	F	df	F
Main effects	13	2.79**	13	3.18***	13	2.04*
Shrub	2	2.07	2	8.26***	2	2.15
Herb	3	2.77*	3	3.03*	3	2.62
Lichen	4	4.12**	4	2.35	4	3.38*
Graminoid	4	0.46	4	1.89	4	0.23
Total	199		199		199	

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

Table 24 summarizes the MCA statistics of the microhabitat analysis. The proportion of variance in the dependent variable explained by all predictors together is given by the multiple R^2. The predictors explained 12, 15, and 19 percent of the variance in the abundance of S. arcticus, M. hoyi, and S. cinereus, respectively. The eta^2 coefficients indicate that lichen cover by itself explained 10% and 6% of the variation of M. hoyi and S. arcticus abundance, respectively. Shrub and herb cover each explained 5% of the variance in the abundance of S. cinereus. The rank order of the betas indicate the relative importance of the various predicators in their explanation of the dependent variable while holding constant all other predictors. Graminoid cover was of negligible importance as a determinant of species abundance after other predictors had been taken into account; its beta coefficients are between 0.07 and 0.19. The best predictors of abundance for M. hoyi, S. cinereus, and S. arcticus are lichen, shrub, and lichen, respectively.

The major interpretation in MCA is of the adjusted coefficients which are expressed as deviations from the overall mean (grand mean - least squared mean) for each subclass of the predictor variables. A positive coefficient indicates that a greater than average number of animals were caught in a cover class while a negative value indicates fewer captures than the average. The pattern of the effects

Table 24. Summary of MCA statistics of vegetational cover predictors in relation to the abundance of the shrew species.

Predictor	Statistic	*M. hoyi*	*S. cinereus*	*S. arcticus*
Shrub	Eta	0.07	0.23	0.12
	Eta^2	0.01	0.05	0.01
	Beta	0.13	0.28	0.14
Herb	Eta	0.21	0.23	0.19
	Eta^2	0.04	0.05	0.04
	Beta	0.20	0.22	0.21
Lichen	Eta	0.32	0.21	0.25
	Eta^2	0.10	0.04	0.06
	Beta	0.31	0.25	0.27
Graminoid	Eta	0.15	0.14	0.07
	Eta^2	0.02	0.02	0.01
	Beta	0.09	0.19	0.07
	Multiple R^2	0.15	0.19	0.12

of those predictor variables that were significant for at least one species in the analysis of variance is presented in Figure 14. MCA coefficients increased with increasing shrub and herb covers. As lichen cover increased MCA coefficients tended to decrease except for S. arcticus which increased in the 76 to 100 percent lichen cover class. This indicates that shrews selected areas with dense ground cover and avoided dense lichen cover, except for S. arcticus which seemed to prefer these dry sites as well as moist areas.

To test the significance of the trends observed in Figure 14, shrew abundance was compared with the cover classes of each predictor separately by means of Duncan's multiple range test (Table 25). All shrews were significantly more abundant in the 26 to 100 percent herb cover class than in the lower classes. S. cinereus was taken in significantly higher numbers in the 26 to 100 percent shrub cover class. The other species showed no significant differences in numbers for shrub cover. M. hoyi and S. cinereus were caught in significantly higher numbers at low lichen cover classes than at high ones. There was no significant difference between low and high lichen cover classes for S. arcticus, indicating a preference for both dry and wet microhabitats within lowland areas. This confirms the microhabitat analysis which found that S. arcticus showed a preference for moist areas but was also able to tolerate dry areas. Shrews, in general, seem to prefer moist conditions under a dense ground cover.

Figure 14. Abundance patterns of M. hoyi, S. cinereus, and S. arcticus in relation to shrub, herb, and lichen cover.

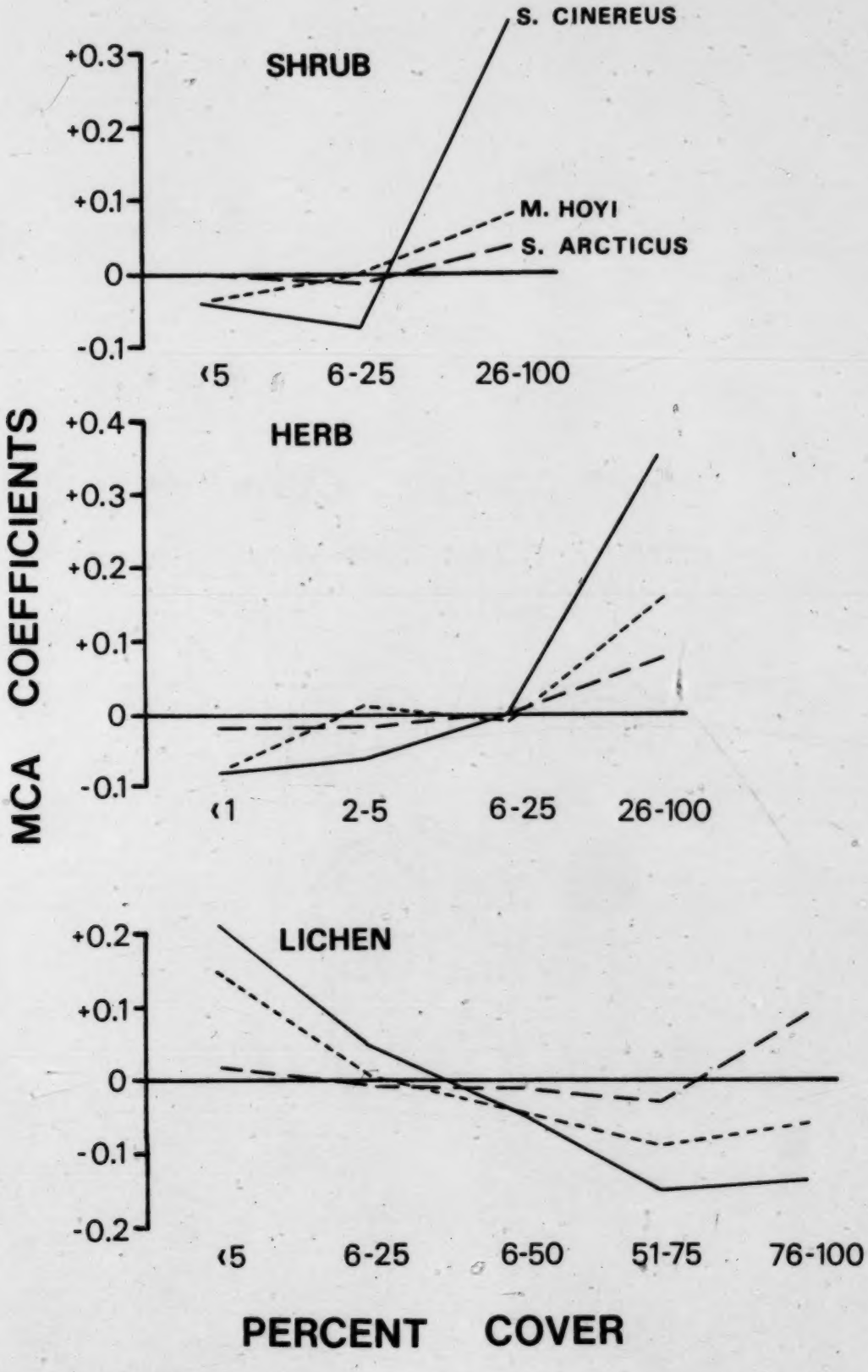

S. CINEREUS
SHRUB
+0.3
+0.2
+0.1
0
-0.1
M. HOYI
S. ARCTICUS
‹5
6-25
26-100
MCA COEFFICIENTS
HERB
+0.4
+0.3
+0.2
+0.1
0
-0.1
‹1
2-5
6-25
26-100
LICHEN
+0.2
+0.1
0
-0.1
-0.2
‹5
6-25
6-50
51-75
76-100
PERCENT COVER

Table 25. Significance of differences between cover classes of shrubs, herbs, and lichens, and the abundance of three shrew species using Duncan's multiple range test. Classes joined by the same horizontal line do not differ at the $p < 0.05$ level of significance. Numbers are percentages.

	Shrub			
	<5	6-25	26-100	
M. hoyi	———	———	———	
S. cinereus	———	———		
S. arcticus	———	———	———	
	Herb			
	<1	2-5	6-25	6-100
M. hoyi	———	———	———	
S. cinereus	———	———	———	
S. arcticus	———	———	———	
	Lichen			
	51-75	76-100	26-50	6-25 <5
M. hoyi	———	———	———	
S. cinereus	———	———	———	———
	51-75	26-50	6-25	<5 76-100
S. arcticus	———	———	———	———

Discussion

It is clear that shrews are easily caught in pitfall traps and that this type of trapping program gives a better indication of species composition and relative abundances of insectivores in small mammal communities than the more conventional methods of snap-trapping and/or live-trapping (Buckner 1957; MacLeod and Lethieq 1963; Brown 1967; Pucek 1969). Such removal methods have been commonly used in small mammal population studies in Europe (Grodzinski et al. 1966; Pucek 1969). Removal trapping of any type for a prolonged period has effects on relative proportions and population structure of the species caught. In the present study, removal trapping created a gap in the community's dominant small mammal populations which was quantitatively filled by dispersing animals before the next trapping period. The structure of the population of S. cinereus on the grids differed from that of the general population (Table 10). It would also be expected that dispersing M. pennsylvanicus and C. gapperi would differ from the general population in age and sex composition as Kozakiewicz (1976) found in bank voles (Clethrionomys glareolus). M. hoyi, S. arcticus, and S. obscurus dispersed onto the grids to a much lesser extent than S. cinereus, and no significant differences in their population structure were observed.

Variation in the numbers of animals dispersing onto the

grids seemed to reflect the variation occurring in their population numbers as demonstrated by Kozakiewicz (1976) in C. glareolus. Though the numerical indices were of a different magnitude, the seasonal population changes of S. cinereus and M. hoyi on the grids were similar to those on the trap lines. Grids, pitfall trap lines, and upland snap-trap lines all showed S. cinereus numbers peaking in 1977. Though S. arcticus was only caught occasionally on the grids, its numbers showed an increase in 1977, but since none were caught on trap lines until 1977 no comparison can be made between grid and trap line numbers for 1976 and 1977. The numbers of the rare S. obscurus seemed to remain stable. Contrary to Buckner (1966), who found the numbers of sympatric populations of S. cinereus and S. arcticus to vary inversely, the present study would indicate that they are in synchrony but at different levels. Similar differences in the relative abundance of sympatric shrews were found by Spencer and Pettus (1966). In their study, S. cinereus and S. vagrans peaked and declined synchronously in numbers, while S. nanus and M. hoyi numbers remained stable. Concurrent studies of C. gapperi in upland areas revealed the same numerical trend (Fuller, unpublished data) as that on removal grids. Although there were no studies with which to compare M. pennsylvanicus numbers from the grids, the trends observed probably reflected the variations occurring in its population numbers.

Shrews as well as microtines have an enormous potential for numerical increase which is seldom fully expressed. Litter sizes of M. hoyi, S. cinereus, and S. arcticus all averaged about eight (Table 8). After the first litters are born, a postpartum estrus is possible, as shown for S. araneus (Brambell 1935) and Blarina brevicauda (Pearson 1944). This would mean that a second litter could be born about the same time as the first litter is weaned. This, coupled with the ability of YY females to breed in their first year, could cause numbers to increase rapidly. During the present study, however, I caught no pregnant, lactating females, so I have no evidence of a successful postpartum estrus. Sexually mature YY females of all shrew species were captured only in 1977 when S. cinereus numbers peaked. Though all shrew species seemed to have about the same reproductive potential, only S. cinereus came close to realizing this potential in 1977. The other species remained at relatively low population levels.

Maturation of YY females, as observed in 1977, has previously been reported for S. cinereus (Buckner 1966) and for S. araneus and S. minutus (Pucek 1960). It appears that only first litter females mature sexually when this phenomenon occurs and they are able to give birth to more than one litter. This is in agreement with Pucek (1960), except that he found no evidence of a difference in the size of litters born to YY and OW females, perhaps because of the small size of his samples of breeding YY females. The

maximum proportion of YY females observed to be breeding was 22% in Pucek's study, whereas they made up 64.9% of the breeding female population in my study in 1977. Thus in certain years the sexual maturation of YY females can be very important to the population dynamics of the species.

Unlike YY females, YY males generally do not mature sexually in their first summer (Pearson 1944; Pucek 1960) although they are known to mature regularly under laboratory conditions (Pearson 1944; Blus 1971). One sexually mature YY S. araneus male was reported from a wild population in Europe by Kowalska-Dyrez (1967). It appears that YY males usually mature in the spring of their second year and remain in breeding condition until they disappear from the population that fall. The aggressive behaviour of mobile breeding OW males may, as in the case of voles (Viitala 1977), inhibit the maturation of YY males.

Seasonal changes in body size and cranial height in M. hoyi, S. cinereus, and S. arcticus are similar to those observed in S. araneus from Europe. The change in these measurements is a phenomenon that has been interpreted as an adaptation to limited food supplies in areas with long, cold winters (Mezhzherin 1964; Pucek 1970).

It is well known that body weight and length of Palearctic shrews decreases over winter (Dehnel 1949; Crowcroft 1957; Pucek 1970). The decrease in weight is the result of a decrease in cellular water, which is probably

related to a lowering of metabolic activity (M. Pucek 1965). This smaller body size allows shrews to overwinter with a decrease in the absolute amount of food required, though the relative amount is increased (Mezhzherin 1964; Pucek 1970). Body length reduction is caused by changes in the intervertebral discs (Hyvarinen 1969).

The body weight of M. hoyi and S. cinereus decreased 23.3% and 19.5%, respectively, from August into winter. This is more or less comparable with the 32.1% decline in the weight of S. araneus from Poland (Z. Pucek 1965). In spring, with the onset of breeding, shrews nearly double their weight; M. hoyi and S. cinereus increased 91.7% and 92.7% in body weight, respectively. Z. Pucek (1965) reported a comparable 106.7% increase in weight for S. araneus from February to June. Changes in body weight have been reported for the vole, C. gapperi, in the Heart Lake area by Fuller (1969, 1977b).

Pucek (1960) concluded that body length did not change in response to sexual maturity in YY females but was a function of age and season. My data (Table 5) indicate that breeding YY females were significantly longer than non-breeding young but significantly shorter than OW females. This agrees with Shvarts (1962) and Hawes (1975), and suggests that body length is affected by reproductive condition, age, and season or that only the largest individuals mature. Dehnel (1952) explained the sexual

maturation of YY females in terms of their food supply which can be extremely variable. YY females may mature in response to holding a territory with optimal food conditions which would also promote growth, resulting in large, sexually mature individuals. When no space is available for new territories, maturation may be inhibited by a physiological mechanism as in mice (Christian 1955). It would follow that first litter females would be the ones to mature in years like 1977 when there was plenty of space because flooding was minimal.

Variation in cranial height has been attributed to age (Jackson 1928; Rudd 1955) and seasonal variation (Dehnel 1949). Pucek (1963) showed that the decrease in skull height was due to reabsorption of bone at the sutures during winter and new bone growth in spring. My results indicated an age difference as well as a seasonal difference in cranial height. There was a significant difference in cranial heights of OW and YY S. cinereus and a similar pattern was observed in S. arcticus and M. hoyi although the differences were not significant. Cranial height was lowest in winter, increased in spring, and reached a mean value for OW animals that was significantly lower for S. cinereus and M. hoyi than the mean of the same cohort the previous summer when they were YY animals. Thus, the observed age difference in cranial height can be explained in relation to seasonal variations.

Pucek (1963) found a 17 percent winter reduction in cranial height in S. araneus from U.S.S.R., Bulgaria, and Czechoslovakia which is comparable to the 17 percent reduction in S. cinereus in the present study. M. hoyi showed a reduction of 25 percent.

The findings of the present study have shown that the seasonal morphological changes in shrews known as Dehnel's phenomenon also occur in Nearctic species of the genera Sorex and Microsorex. This suggests that Dehnel's phenomenon is probably characteristic of all Holarctic species of shrews.

Extreme winter conditions make heavy energetic demands on shrews as well as other small mammals that remain active under the snow cover. The lower absolute energy requirements associated with the winter decrease in size of shrews and rodents must more than offset any increased thermoregulatory cost.

Fluctuations in numbers of M. pennsylvanicus and C. gapperi were synchronous but they were out of phase with S. cinereus. Although these small rodents were exposed to the same microclimatic conditions as S. cinereus, their numerical response was totally different. An explanation for this difference may lie in the different trophic levels occupied by the two groups. Voles, being herbivores, are primary consumers. The insectivorous diet of shrews makes their assignment to any single trophic level difficult

because their energy requirements come from various sources, but in general I would classify them as secondary - tertiary consumers. This basic dietary difference is probably fundamental to the observed difference in population numbers.

At least three periods of the year have been classed as "critical" to small mammals that remain active throughout the year. These are the fall critical period (Pruitt 1957), spring critical period (Fuller 1967), and mid-winter conditions (Pruitt 1957), which correspond in this study to the periods of fall transition, spring thaw, and deep snow, respectively. As the population numbers were in contrast so were the winter conditions preceeding the two summers of the study (Fig. 4). The winter of 1975-76, with its short fall transition period, rapid accumulation of snow and resulting warm stable subnivean temperatures, could be described as "favourable". The winter of 1976-77, in contrast, had a long fall transition period and cold, fluctuating subnivean temperatures as a result of the slow snow accumulation. These conditions are definitely "harsh" in reference to the temperature regime that small mammals might be exposed to. There was one micrcenvironment, however, that did not change. Subterranean temperatures remained constant during the two winters. If just the vole populations had been studied it would be easy to state that severe winter conditions of 1976-77 were responsible for their decline, but S. cinereus population numbers increased dramatically.

Why would shrews, which are probably more sensitive to changes in temperature because of their high surface to volume ratio than the larger microtines, survive better than voles?

It has already been observed by other authors that vole survival can be exceptionally high during what are thought to be "harsh" winter thermal conditions (Whitney 1976; Fuller 1977a). Conversely, high mortality has occurred in small rodent populations during so called "favourable" conditions when the snow cover was deep and subnivean temperatures were relatively warm and stable (Beer 1961; Fuller 1977a). There are also examples of high survival of rodents during the fall transition period (Fuller et al. 1969; Whitney 1976). These fluctuations in small mammal population numbers occurred in the present study even with a stable year-round subterranean microclimate available, indicating that stable thermal conditions alone are not able to explain population numbers at the start of the breeding season and thus further population increases. Winter conditions with their variable effect on the subnivean thermal regime are also insufficient to explain changes in shrew or rodent populations.

Probably spring thaw is the most important of the periods because the onset and success of breeding along with later recruitment may be affected as indicated by Fuller (1969). However, poor spring survival can occur in years of

high population growth (Whitney 1976). Krebs and Myers (1974) concluded that subsequent population growth is not dependent on survival during the spring period. Therefore, it would seem that microclimate alone is not able to explain fluctuations in population numbers of either shrews or voles. In winter, food becomes a finite resource which declines as time passes. Availability of invertebrate prey, in the case of shrews, is reduced as a result of them becoming inactive and less abundant. In the case of rodents plant productivity ceases and for both the snow cover physically limits the effectiveness of foraging. Thus the overwinter survival rate as well as the seasonal population growth would seem to depend on whether the animals can successfully meet their energy requirements. Mezhzherin (1964) has shown that shrews can withstand prolonged exposure to temperatures (-5°C) similar to those in the subnivean environment if food is present. Therefore it is hypothesized that shrew populations are regulated by the energy limitations imposed by their environment, especially during the winter period which annually limits their distribution and their spring population levels.

Generally shrews show a preference for habitats that are moist and provide dense cover (Getz 1961; Miller and Getz 1977; present study). Considering the importance of food in explaining the specialization of shrews, the distribution and abundance of the soil invertebrate fauna should be related to the habitat preferences of shrews.

Shrub birch fens have dense cover of deciduous shrubs, are always moist, and the soil has a mull litter layer from the decomposition of deciduous leaves. There are no other habitats in the Heart Lake area that have this soil richness. Black spruce fens have a mor litter composed of acidic, partly decomposed peat material sharply separated from the underlying mineral soil. Upland areas also have a mor litter but it is thin and usually over bedrock. From the woodland soil study of Bornebusch (1930) it is known that mor litter supports a small biomass of numerous microarthropods such as mites and Collembola. The richer mull litter has a greater biomass and diversity of larger but relatively less numerous invertebrates than mor litter. Therefore, potential prey available to shrews is greater in biomass, individually larger, and should give shrews a greater energy return per prey item in mull litter than mor litter.

The major part of shrub birch fens were flooded in 1976 and thus unavailable to shrews. The low water table in 1977 opened this habitat to shrews, particularly S. cinereus and S. arcticus which increased in numbers. From these centers of population growth, S. cinereus and S. arcticus dispersed into nearby marginal habitats.

The evidence for dispersal in the present study came from the difference in age between animals caught on grids and on trap lines. The majority of the shrews, except for M.

hoyi, captured on the grids were YY animals with an even sex ratio. YY individuals were also predominated in the catch from upland areas. Trap lines caught more breeding OW animals and fewer YY animals than the grids. Dispersers, in the case of S. cinereus and S. arcticus appeared to emigrate into nearby marginal black spruce habitats first and into unsuitable upland areas last. This was confirmed for S. cinereus by the dates on which YY animals were first captured in the various habitats. No animals were captured on the removal grids until early August in 1976. It was two weeks later that YY animals or any shrews were taken in surrounding uplands. The same sequence of events occurred in 1977 but the dates were earlier as S. cinereus population numbers built up faster than in 1976. The first YY individuals were caught at the end of June on the removal grids and by fall S. cinereus was abundant and found in every habitat, but by the spring of 1978 it was again absent on the removal grids and in all upland areas (S. Pickering, pers. comm.). In all three springs S. cinereus appeared to have a very limited distribution, likely confined to certain optimal habitats in which it was able to overwinter successfully.

The catch of S. arcticus consisted of only three individuals in 1976, all from grids, but when trap line locations were changed in 1977 to shrub birch fens it was caught regularly. It was not until early August that YY animals were caught on grids suggesting that it took longer

for S. arcticus numbers to build up to a level where dispersal would occur than it did for S. cinereus. M. hoyi seemed to prefer wooded black spruce fens as it was the only shrew species caught on the grids when the study started in the spring of 1976. The numbers taken on the grids remained constant over the two years, though a slight peak was observed in 1976. M. hoyi like S. arcticus was caught regularly on the trap lines in shrub birch fens.

Studies on S. araneus and S. minutus by Michielsen (1966) and S. vagrans and S. obscurus by Hawes (1977) have shown that these species are territorial, that is, they have contiguous non-overlapping home ranges. YY animals of these shrew species disperse immediately after leaving the nest and attempt to establish territories which they seem to need in order to overwinter successfully. Hawes (1977) suggested that the effect of territoriality was to regulate population numbers before food became limited, as in winter. In the present study, territoriality may have placed an upper limit on S. cinereus numbers in shrub birch fens as indicated by the dispersal of large numbers of YY animals in 1977, thus ensuring the survival of a portion of the population during winter.

Two different types of dispersal have been recognized by Lidicker (1975): saturation dispersal which occurs when a population is near its carrying capacity and pre-saturation dispersal which occurs during population growth before

saturation occurs. The type of dispersal found in shrews that occurs immediately after YY animals leave the nest and is governed by territorial behavior is pre-saturation dispersal. As suggested by Lidicker (1975) this type of dispersal would probably evolve so that dispersing individuals would have a better chance of surviving and passing on genetic material or so that seasonally isolated populations would be able to interchange genetic material.

Fall snap-trapping conducted by Formozov (1946) showed that shrews could be taken in all habitats when numbers were high but only in certain habitats when their numbers were low. Pruitt (1959) concluded that physical factors were responsible for habitat expansions and contractions observed in Blarina populations. The present study argues that it is the energy deficiencies of habitats that make them unsuitable for shrews. Physical factors such as the flooding of shrub birch fens in 1976 can sometimes be responsible but more often it is probably the abundance of prey that controls the distribution of shrews. Most animals readily disperse into what are probably only seasonally suitable habitats and few are able to survive till spring. Thus, yearly fluctuations observed in some shrew populations seem to be the result of fluctuating prey numbers. The energy limitations imposed by winter conditions, however, seem to act as a yearly check on shrew populations, controlling their numbers and limiting their distribution. Only a certain portion of the population is able to fulfill its

energy requirements and survive the winter, while the energy availability during the snow-free period governs the level of population growth for a particular year.

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